Habitat Area Requirements of Prairie Wetland Birds in Eastern South Dakota

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HABITAT AREA REQUIREMENTS OF PRAIRIE WETLAND BIRDS

IN EASTERN SOUTH DAKOTA

BY

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HABITAT AREA REQUIREMENTS OF PRAIRIE WETLAND BIRDS IN EASTERN SOUTH DAKOTA

This dissertation is approved as a creditable and independent investigation by a candidate for the Doctor of Philosophy degree and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this dissertation does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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Abstract

HABITAT AREA REQUIREMENTS OF PRAIRIE WETLAND BIRDS IN EASTERN SOUTH DAKOTA

David E. Naugle

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The influence of area and vegetation structure on bird use of 830 semipermanent and seasonal wetlands (0.2-217.5 ha) was studied to evaluate vegetative needs and habitat area requirements of 20 breeding wetland bird species in eastern South Dakota in 1995-1996. Vegetative preferences of species varied, but most waterfowl and nongame species occur e4i more frequently in wetlands with intermediate cover-to-water ratios whereas five over-water nesting or secretive nongame species were found in wetlands with greater coverage of emergent vegetation. The occurrence of four nongame species that depend on vegetative structure to support the weight of their over-water nests also was positively associated with semipermanent wetlands dominated by thick-stemmed emergent vegetation (e.g., cattail *[Typha* spp]). Upland land use influenced waterfowl habitat use as the percentage of untilled uplands was 10.4% higher near semipermanent wetlands in which dabbling duck species richness was at a maximum compared to wetlands without dabbling ducks. Despite the importance of wetland and upland vegetation, multiple and logistic regression analyses indicated that wetland area was the best single predictor of

species richness and of habitat use by individual species. Fifty-five to 100% of explained variation was attributed to area (partial R^2 = 0.10-.048) while the occurrences of 95 and 79% of species in semipermanent and seasonal wetlands, respectively, were positively associated with wetland area.

To further investigate the importance of wetland area, I used logistic regression and probability theory to estimate area requirements of individual species, investigate the importance of small wetlands, evaluate potential effects of landscape type on species occurrence, and determine minimum wetland areas needed to preserve multiple area-dependent species. Smaller semipermanent wetlands were predominantly occupied by area-independent species and by species whose area-dependency (50% probability of occurrence) was low (0.2-4.9 ha), whereas larger wetlands generally had a higher diversity composed of species whose area requirements ranged from 0.2-164.8 ha. Lower minimum area requirements and higher average occupancy rates in seasonal compared to semipermanent wetlands for five dabbling duck species indicated that small seasonal wetlands provided extensive breeding habitat for upland nesting waterfowl. Small seasonal wetlands also provided habitat comparable to that of larger semipermanent wetlands for three species of breeding nongame birds. Occurrences of seven bird species that were positively associated with total area of semipermanent and seasonal wetlands indicated that those species were more likely to be found in wetlands that were near other wetlands compared to isolated wetlands. Occurrences of black terns *(Chlidonias niger)* and American coots *(Fulica americana)*, which fluctuated in response to landscape structure, indicated that low wetland density landscapes composed primarily of small wetlands did not provide suitable breeding habitat compared to high wetland density landscapes that contained a mixture of large and small wetlands. Over the range of semipermanent wetlands surveyed, the probability of finding at least eight area-dependent species in an 8-ha semipermanent wetland exceeded 0.50 when area was used as the sole management criterion. Despite the importance of small wetlands to dabbling ducks and area-independent nongame birds, it was unlikely that any number of small wetlands, no matter how well placed within landscapes, could provide suitable habitat for species that only use large wetlands.

My results indicated that attributes within wetlands (e.g., percent vegetated wetland area, stem structure of emergent vegetation) as well as landscape-level attributes surrounding particular wetlands (e.g., proximity of nesting wetlands to other wetlands, proportion of upland grasslands near nesting wetlands) influence bird use of prairie wetlands. To my knowledge, this study also provides the only empirical information concerning minimum habitat area requirements for wetland birds, a parameter which estimates the likelihood of providing for even minimum populations of individual species and is an important component in developing prescriptive management recommendations for wetlands conservation. The identification of five area-independent nongame species in this study indicated that every seasonal wetland, regardless of its area, represents valuable breeding habitat for some wetland avifauna. Large semipermanent wetlands (>95 ha) embedded in contiguous tracts of upland grasslands were the only wetlands large enough to support breeding populations of species requiring the greatest wetland area. In parts of eastern South Dakota that are largely devoid of semipermanent wetlands, smaller seasonal wetlands provided extensive habitat for dabbling ducks and for 10 species of nongame birds with minimum wetland area requirements of <3.3 ha.

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CHAPTER 1

FACTORS ASSOCIATED WITH BIRD OCCURRENCE

IN SEMIPERMANENT AND SEASONAL WETLANDS

Introduction

In a little over a century, the prairie pothole region of the northern Great Plains has been transformed from a contiguous expanse of wetlands and grasslands into a highly fragmented, agricultural landscape that is less conducive to wetland bird production. In a region where wetland losses due to drainage have been high (Dahl 1990), South Dakota is one of the few prairie states that still has a majority (-65%) of its wetlands. Wetland ecosystems provide the principal breeding and foraging habitats for about one-third of North America's avifauna, most of which are nongame species (Kroodsma 1978). As human alterations of the landscape continue to increase the need for management of prairie wetlands, resource managers require more information concerning wetland habitat requirements of waterfowl and nongame species.

Early research concerning wetland bird habitat use associated the distribution and abundance of many wetland species to variation in vegetative cover within wetlands (e.g., Weller and Spatcher 1965). More recently, researchers have used principles of island biogeography theory (MacArthur and Wilson 1967) to associate bird species richness to wetland area and isolation (Tyser 1983, Brown and Dinsmore 1986, Gibbs et al. 1991). Although previous investigations have indicated that wetland birds relate to area and isolation, as well as vegetation parameters in wetlands, little information describing area-dependency of individual species is available.

The objective of this study was to identify attributes of semipermanent and seasonal wetlands associated with bird species richness and the occurrence of individual wetland bird species. In addition to hypothesizing that species richness and the occurrence of individual species would be associated with vegetative characteristics of wetlands, I also hypothesized that birds would relate to wetland area and isolation measures. In this chapter, I present predictive models that identify habitat attributes associated with bird species richness and the occurrence of individual wetland bird species. I also present estimates of the relative influence of wetland area on bird species richness and provide information pertaining to the number of wetland species whose occurrence is related to wetland area.

Study Area

This study was conducted in six physiographic regions of eastern South Dakota (Johnson et al. 1995) that were modified into three domains (Fig. 1) encompassing areas with similar wetland characteristics (Kantrud et al. 1989). Allocation of total surface area in eastern South Dakota across domains was 28.7% in Prairie Coteau, 44.3% in Central Lowlands, and 27.0% in Missouri Coteau (Fig. 1). Wetlands and deep-water habitats cover 899,000 ha (9.8%) of the 91,600 km^2 in eastern South Dakota (Johnson and Higgins 1997). This area includes 334,699 seasonal wetlands covering 224,004 ha and 24,485 natural, semipermanent wetlands covering 173,010 ha that were available for use by prairie wetland birds (Johnson and Higgins 1997).

Wetland characteristics within sampling domains of this study were influenced by recent glacial advances that retreated only 10,000 years ago. Johnson and Higgins

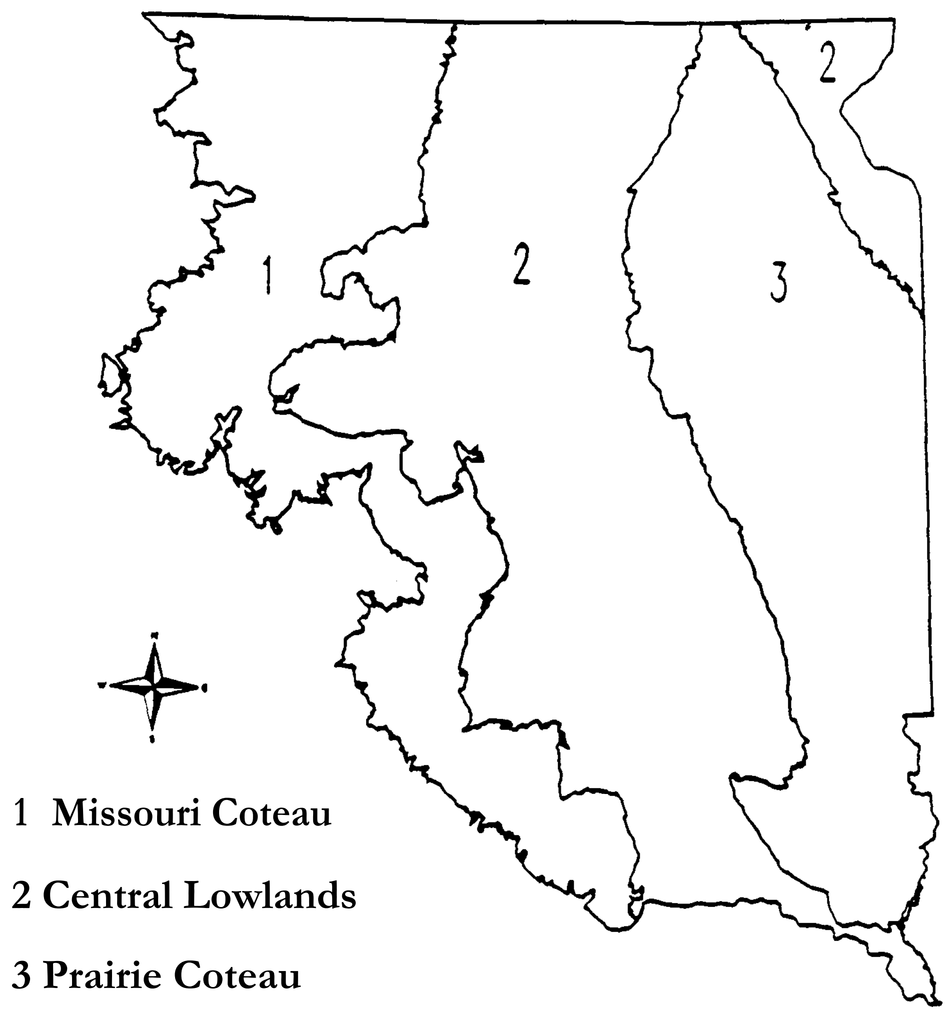

Fig. 1. Three domains (Missouri Coteau, Central Lowlands, Prairie Coteau) that were delineated for surveying wetlands in eastern South Dakota. Domains are modifications of six major physiographic regions (Johnson et al. 1995).

(1997) provided a detailed description of glacial episodes and their resulting influences on wetland characteristics throughout my study area. In general, the Missouri Coteau is a moderate relief landscape that has an abundance of temporary and seasonal wetlands in the northeast and a low density of fluviatile wetlands throughout the south and west. The Central Lowlands is a low relief landscape with high densities of seasonal and temporary wetlands. The Prairie Coteau, which has the highest topographic relief, is characterized by an abundance of large semipermanent and permanent wetlands with an interspersion of temporary and seasonal wetlands.

Highly variable wet-dry cycles (Winter 1989) make wetland conditions inherently unpredictable in the prairie pothole region of eastern South Dakota. Wet hydrologic conditions that occurred throughout the study area during both years of this study kept seasonal and semipermanent wetlands inundated during summer months. Native upland vegetation throughout eastern South Dakota is tall-grass/mixed-grass prairie (Westin and Maio 1978). Abundance of native and introduced grasslands (e.g., Conservation Reserve Program fields) varies locally and regionally. Regional grassland abundance is highest throughout the Missouri Coteau and in northerly portions of the Prairie Coteau. Farming is intensive in the remainder of the Prairie Coteau and throughout the Central Lowlands where small grains and row crops have replaced native upland vegetation. Primary crops are wheat *(Triticum aestivum),* soybeans *(Glycine max),* and corn *(Zea mays).* Trautman (1982) provided a detailed description of land use across the region. Land ownership is predominately private interspersed with state-owned parks (n=12), game production areas (n=573; 63,600 ha), federally-owned national wildlife refuges (n=2), and waterfowl production areas (n=763; -65,200 ha) (K. K. Bakker and K. F. Higgins, unpubl. data, South Dakota State University).

Methods

<u>Wetland Selection Process</u>

A grid composed of 3,800, 25.9 km^2 (10 mi^1) cells was overlayed on a geographic information system (GIS) that was constructed from National Wetland Inventory (NWI) data for eastern South Dakota (Johnson and Higgins 1997). Cell size (25.9 km^2) was selected to maximize between cell variability (Stoms 1992). Cells (n=216) were selected randomly in equal numbers across landscape types within the Prairie Coteau, Missouri Coteau, and James River Lowlands regions of eastern South Dakota (Fig. 2). Wetland centers were used to assign wetlands that fell in multiple cells to a particular cell. Median values of the frequency distributions of semipermanent and seasonal wetland densities (110 wetlands) and areas (124 ha) were used to define four distinct landscape types (Fig. 3). Landscape type a (Fig. 3) was low wetland density and area, Landscape b low density and high area, Landscape c high density and low area, and Landscape d cells were high density and area (Fig. 3). Cells within landscape types were numbered sequentially. Seasonal and semipermanent wetlands within cells were sorted by area. Wetlands that were sorted by area were systematically selected using a random starting point to ensure that wetlands were evenly distributed by area. Wetlands that were dry, farmed, burned, mowed, or hayed were not sampled. Bird surveys were conducted in two seasonal and two semipermanent wetlands per cell after landowners were contacted to obtain access to wetlands.

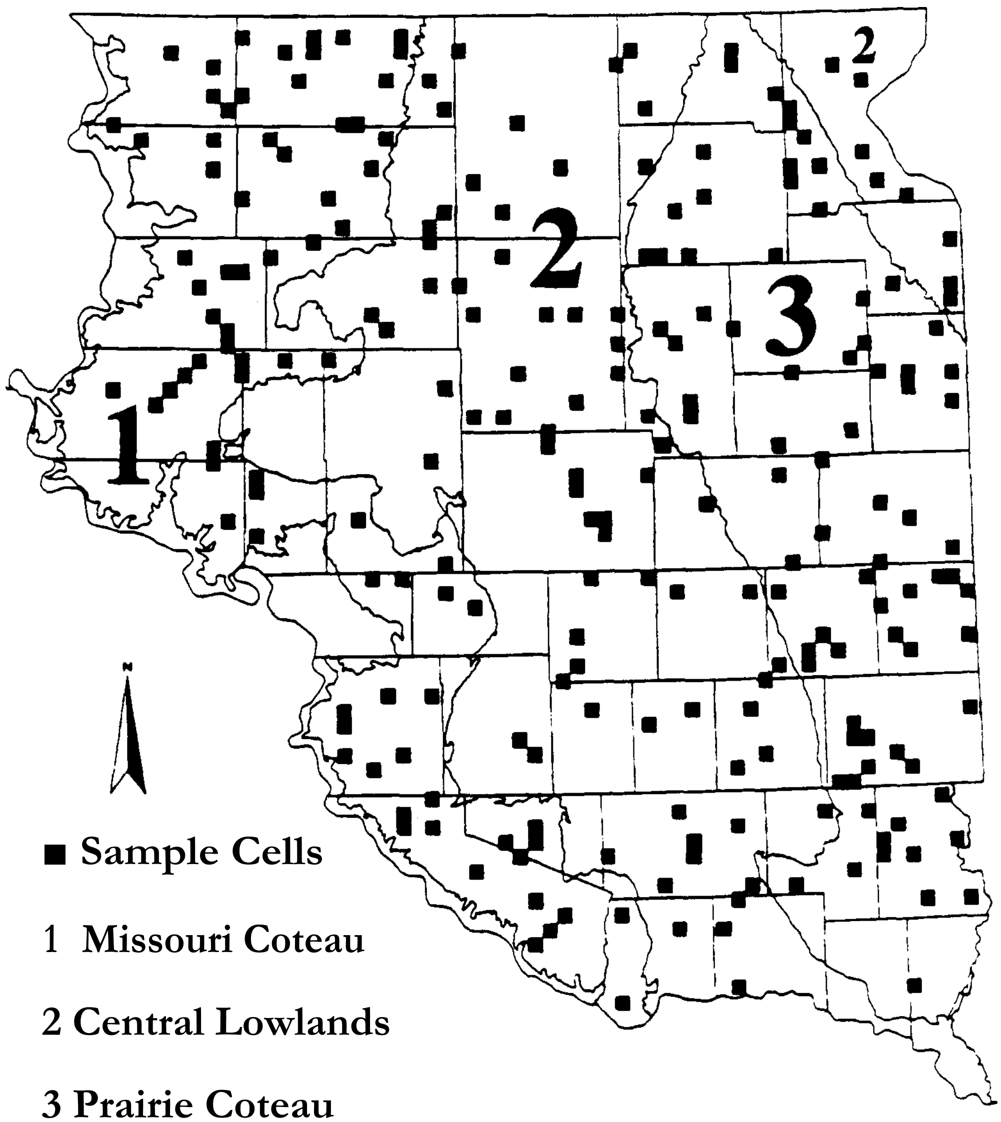

Fig. 2. Distribution of 25.9 km^2 (10 mi^1) cells that were used to evaluate prairie wetland bird use of seasonal and semipermanent wetlands in the Missouri and Prairie Coteaus and Central Lowlands regions of eastern South Dakota, 1995 and 1996.

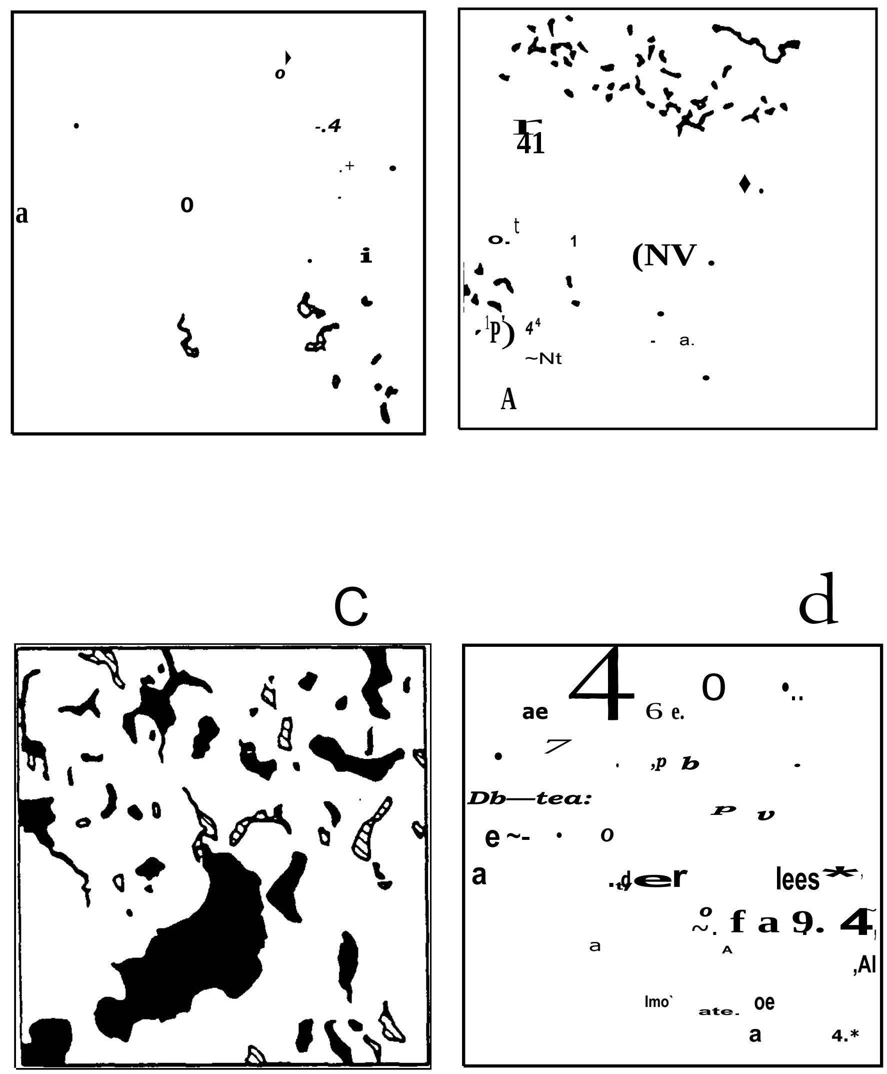

Fig. 3. Examples of the four types of landscapes used to characterize the wetland community surrounding surveyed wetlands. Solid polygons depict semipermanent wetlands while hatched polygons are seasonal wetlands. Each of four squares are 25.9 km^2 (10 mi^1) in area.

Bird Surveys

Survey methodology generally followed an established sampling protocol that has been used extensively to survey birds in wetlands (Brown and Dinsmore 1986, Hemesath and Dinsmore 1993, VanRees-Siewert and Dinsmore 1996). Bird species that were seen or heard were recorded during 8-minute surveys (Scott and Ramsey 1981, Fuller and Langslow 1984) within 18-m (0.1 ha) fixed radius circular-plots (Reynolds et al. 1980, Edwards et al. 1981, Brown and Dinsmore 1986). In addition to recording conspicuous birds that were seen or heard during the 8-minute surveys, tape recordings of Virginia rail (see Appendix 1 for scientific names not listed in text), sora, least bittern *(Ixobrychus exilis),* and American bittern calls were played to elicit responses from these secretive species (Marion et al. 1981, Johnson and Dinsmore 1986, Gibbs and Melvin 1993). Observers waited two minutes within circular-plots before beginning surveys to allow birds to return to their normal behavior (Bollinger et al. 1988).

Birds were surveyed in 1-4 circular-plots, depending on wetland area (Brown and Dinsmore 1986, Vickery et al. 1994) and number and arrangement of vegetative cover types. Survey coverage of the total wetland area varied from nearly 100% in small wetlands to <1% in large wetlands. Less intensive sampling in large wetlands was compensated for by recording birds detected when moving between plots (Brown and Dinsmore 1986), and those detected outside of circular-plots during surveys (Brown and Dinsmore 1986, Hemesath and Dinsmore 1993). Wetland perimeters also were traversed to ensure detection of all species present. Circular-plots were evenly spaced in emergent vegetation throughout each wetland. When no emergent vegetation was present, circular-plots were placed near the wetland edge and birds were surveyed before approaching the wetland. Wetlands were classified as used by a particular species if adults, active nests, or young were observed. Surveys were conducted when birds were usually most active (sunrise to 1000 hr and 1800 hr to sunset [Skirvin 1981, Verner and Ritter 1986]). Surveys were not conducted during rainy or windy (>24 km/h) days.

Accuracy Assessment of Survey Methodology

Wetlands were surveyed once in 1995 or 1996 to obtain a large sample (n = 830) over an extensive geographic region rather than surveying a small number of localized wetlands multiple times (Meentemeyer 1989). The modification in survey sampling intensity increased the number of wetlands surveyed to meet sample size requirements for logistic regression analyses (Cox 1970). Accuracy of survey methodology was assessed by surveying a random sub-set of 20 wetlands twice within the same sampling season to determine how effectively a single survey characterized the wetland bird community and to determine whether length of time observers spent within wetlands influenced the number of wetland species that were seen or heard. Each second survey was conducted by an observer who did not have prior knowledge of the species that were recorded during the first survey. Observers that surveyed wetlands a second time recorded birds and broadcasted calls of secretive species for 32 min (the length of time required to complete four circular-plots in large wetlands) in smaller wetlands in which <4 circular plots were used.

Vegetative Measures Within and Adjacent to Wetlands

A complete listing of variables that were measured or calculated is presented in Table 1. The proportion of the wetland area containing emergent cover was estimated visually using the Daubenmire (1959) scale in which the entire wetland was treated as a single quadrat (Bailey and Poulton 1968). Class intervals describing the percentage of vegetated area within wetlands were defined as: 1) <1%; 2) 1-5%; 3) 6-25%; 4) 26-50%; 5) 51-75%; 6) >76-95%; 7) >95%. Class interval mid-points were used to analyze categorical data. Spatial distribution of emergent vegetation was classified using the four cover type classifications of Stewart and Kantrud (1971) (Fig. 4).

Grazing intensity within wetlands was visually estimated as light, moderate, or heavy. Wetlands were lightly grazed when there was little or no evidence that cattle had been present within the wetland whereas emergent vegetation in moderately grazed wetlands showed signs of trampling and consumption. Emergent vegetation in heavily grazed wetlands was severely impacted by the presence of cattle. Grazing intensity was estimated on natural shorelines by visual inspection of residual vegetation and current year's growth. Shorelines that ranged from idled (i.e., <1%) to heavily grazed (i.e., >95%) were recorded using the same seven class intervals that were used to estimate percent emergent cover. Proportion of the wetland perimeter occupied by woody hydrophytes (i.e., willow *[Salix* spp.] and cottonwood *[Populus deltoides])* also was estimated visually into one of the seven class intervals. Land use adjacent to surveyed wetlands was classified as tilled or untilled.

Table 1. Description of variables that were measured to evaluate wetland bird use of seasonal and semipermanent wetland habitats in eastern South Dakota, 1995-1996.

Variable Name	Description
AREA[a]	Natural logarithm of the area (ha) of the wetland
PERIM	Natural logarithm of the perimeter (m) of the wetland
TEMPA'	Natural logarithm of the total temporary wetland areas within cells
SEASA[a]	Natural logarithm of the total seasonal wetland areas within cells
SEMIA[a]	Natural logarithm of the total semipermanent wetland areas within cells
PERMA[a]	Natural logarithm of the total permanent wetland areas within cells
TEMPN	Natural logarithm of temporary wetland numbers within cells
SEASN	Natural logarithm of seasonal wetland numbers within cells
SEMIN	Natural logarithm of semipermanent wetland numbers within cells
PERMN	Natural logarithm of permanent wetland numbers within cells
COVER[a]	Percent vegetated wetland area
COVTYPE	Cover type classification [b]
WETGRAZ	Index to grazing intensity within wetlands
SHORGRAZ[a]	Index to grazing intensity on shorelines adjacent to wetlands
GRASS[a]	Proportion of untilled upland habitat within cells
LANDUSE[a]	Dummy-coded variable indicating whether land adjacent to the wetland was tilled or untilled
TREES[a]	Proportion of the wetland perimeter encompassed by woody hydrophytes
STEM'	Variable indicating whether herbaceous hydrophytes within wetlands were predominately thick- or thin-stemmed
VEGNUM'	Number of emergent hydrophytes species composing > 10% of the vegetated wetland area

'Variable was included in stepwise multiple regression analyses and stepwise logistic analyses.

[b] Cover type classifications that follow Stewart and Kantrud (1971) describe the distribution of emergent vegetation within wetlands.

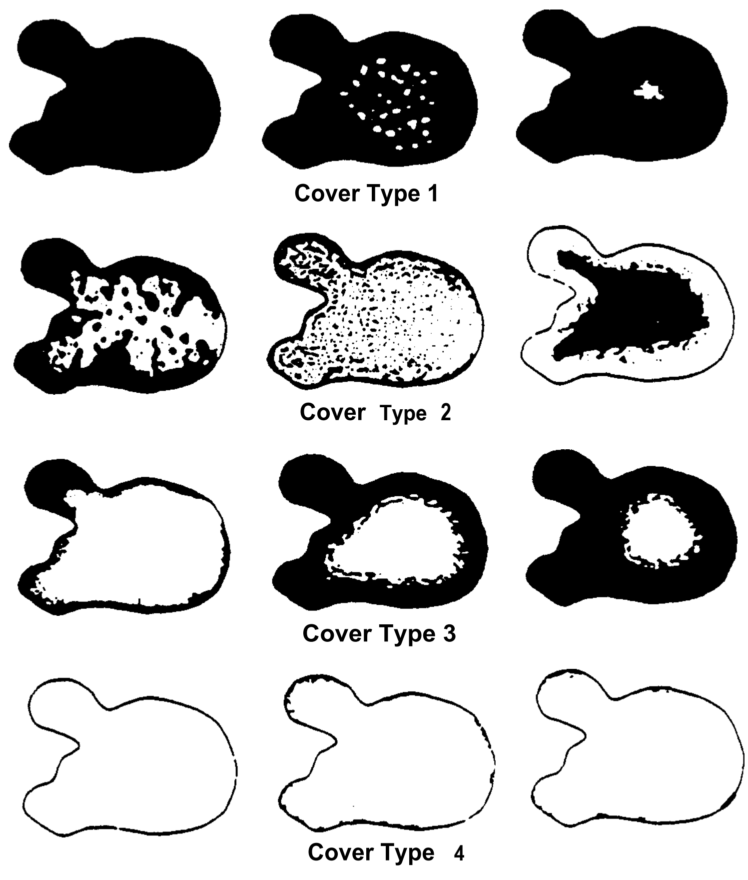

Fig. 4. Four cover type classifications (adopted from Stewart and Kantrud 1971) used to depict the spatial distribution of emergent vegetation in wetlands. Black coloration denotes vegetated wetland area. White coloration is open-water areas.

Number of emergent hydrophytes comprising > 10% of the vegetated wetland area was recorded as an index to wetland vegetation heterogeneity. Emergent cover also was used to categorize wetlands into two classes of nesting substrates for wetland birds. Class 1 substrates were dominated by thick-stemmed emergent vegetation types (e.g., cattail *[Typha* spp.], river bulrush *[Scirpus fluviatilis])* that were capable of supporting the weight of a bird nest, whereas Class 2 substrates were dominated by thin-stemmed emergent vegetation types (e.g., softstem bulrush *[Scirpus tabernaemontani],* burreed *[Sparganium eurycarpum])* whose weaker stems are less capable of supporting a nest.

Wetland and Upland Variables Measured by Remote Sensing

Wetland area (ha) and shoreline length (m) of surveyed wetlands were estimated using a wetland GIS (Johnson 1995). Densities and total areas of temporary, seasonal, semipermanent, and permanent wetlands (Stewart and Kantrud 1971) were calculated within 25.9 km^2 cells to characterize the wetland complex surrounding surveyed wetlands. Wetland area and shoreline length measurements, and wetland density and area measurements were log transformed to approximate normality.

Landsat Thematic Mapper (TM) imagery from eight scenes covering eastern South Dakota were used to classify uplands into tilled and untilled vegetation classes to determine whether abundance of grassland cover within 25.9 km^2 (10 mi^1) cells was related to bird use of wetlands. Crops (e.g., corn, soybeans, wheat) and annually fallowed areas were considered tilled lands. Untilled lands were permanent pastures, Conservation Reserve Program fields, and alfalfa. Trees, which are usually within shelterbelt plantings that constituted <1% of area in eastern South Dakota, were not distinguished from untilled herbaceous grassland cover types.

I used spring imagery (i.e., leaf-off scenes in April and May of 1991 and 1992) that was acquired before row crops had emerged to enhance my ability to differentiate between tilled and untilled uplands. Spectral bands used were visible red (Band 3, 0.63-0.69 µm), near infrared (Band 4, 0.76-0.90 µm), shortwave infrared (Band 5, 1.55-1.75 µm), and thermal infrared (Band 7, 10.4-12.5µm) at a spatial resolution of 30 m. Initial processing of the four spectral bands into one image was completed using ERDAS image processing software on a SUN SPARC 10 workstation. An unsupervised classification (i.e., cluster analysis) was conducted on the 4-band image using the Land Analysis System software (U.S. Geological Survey, EROS Data Center, Sioux Falls, S.D.). Unsupervised classification involved clustering (i.e., shading) individual pixels into 100 spectral classes by measured reflectance values from the TM 4-band image. Spectral classes were then visually interpreted as tilled or untilled land cover units.

A digital coverage depicting land use for a 250 km^2 area of northeastern South Dakota during 1992 (Naugle et al. 1997), the period when TM data for this study were acquired, was used as a reference during land use interpretation. Black and white aerial photographs (1:8,000 scale) depicting certified annual cropping history in 84 randomly selected 1.6 km^2 reference areas located in eastern South Dakota were obtained from the Farm Service Agency (U.S. Department of Agriculture) to enhance the visual land cover interpretation. Half the photographs were used during land use classification; the other half of the photographs, which were not viewed until land use classification had been completed, were used to evaluate the accuracy of the tilled and untilled classifications. Overall, per-pixel classification accuracy (Stoms 1994) for the map was 97%.

Classified imagery was converted from ERDAS to ARC/INFO format. The NWI data in raster format were used to mask out wetland area. Untilled (i.e., upland grassland cover) area estimates were calculated from the classified imagery within 25.9 km^2 cells. Proportion of untilled area was defined as the sum of untilled area divided by the sum of non-wetland area within cells. Percentage data were square-root transformed to approximate normality.

<u>Multiple Regression Habitat Analyses</u>

Stepwise multiple regression was used to analyze relationships between bird species richness and habitat variables. Habitat variables that were highly correlated ($r > 0.5$) with others were removed before performing analyses to minimize problems associated with multicollinearity. Eleven independent variables were included in analyses: wetland area (AREA), total area of temporary (TEMPA), seasonal (SEASA), semipermanent (SEMIA), and permanent (PERMA) wetlands within cells, percent vegetated wetland area (COVER), an index to grazing intensity on shorelines adjacent to wetlands (SHORGRAZ), proportion of untilled upland habitat within cells (GRASS), proportion of the wetland perimeter encompassed by woody hydrophytes (TREES), a dummy variable indicating whether emergent hydrophytes within wetlands were predominately thick- or thin-stemmed (STEM), and the number of emergent hydrophytes composing > 10% of the vegetated wetland area (VEGNUM) (Table 1).

Dependent variables tested were seven estimates of waterfowl (n = 11 species) and nongame bird species (n = 31 species) richness (Appendix 1 details specific species included in richness estimates). For purposes of this study, breeding nongame bird species richness included non-waterfowl species (n = 9) that commonly nest or spend their entire day within semipermanent and seasonal wetlands (Craig and Beal 1992). In contrast, user bird species richness included non-waterfowl species (n = 22) that foraged in wetlands but nested elsewhere (e.g., great blue herons and swallows).

Habitat variables P < 0.05 were retained in forward stepwise models only when their inclusion explained an additional 5% of variation. Variation explained by wetland area was divided by the coefficient of determination for the entire regression equation, which indicated the importance of habitat area. A preliminary comparison of breeding bird species richness did not reveal significant differences between years (P > 0.10); therefore, data from both years were pooled for all analyses. Seasonal and semipermanent wetland data were analyzed separately. Only species that occurred in >10 wetlands were used in species richness estimates. All wetlands surveyed were included in analyses.

Logistic Regression Habitat Analyses

Stepwise logistic regression analyses (Cox 1970, Wilkinson 1997) were used to evaluate relationships between habitat variables and the probability of individual bird species occurrence. To evaluate whether the probability of occurrence of individual species was related to habitat variables (x,;.... x;), I used the model

$$P(y_1 = 1) = \frac{\exp(\beta_0 + \beta_1 x_{1_i} + \beta_2 x_{2_i})}{1 + \exp(\beta_0 + \beta_1 x_{1_i} + \beta_2 x_{2_i})}$$

where $P(y_i = 1)$ is the probability of the particular species being present in wetland i and (3o, p,, and R 2 are model parameters to be estimated. Significance of the regression was tested using the Wald chi-square statistic (maximum likelihood estimate). McFadden's Rho-squared statistic, which was used to evaluate model fit, is a transformation of the likelihood ratio statistic intended to mimic R^2 values in logistic regression. Low Rho-squared values do not necessarily imply poor model fit because Rho-squared are lower than R^2 values. Rho-squared values between 0.20 and 0.40 were considered satisfactory (Hensher and Johnson 1981). Variables that entered stepwise logistic analyses at $P < 0.15$ were retained when $P < 0.01$. Regressions were conducted for bird species that occurred in > 19 wetlands. Seasonal and semipermanent wetland data were analyzed separately. All wetlands surveyed were included in analyses.

Results

Habitat Variables Associated with Species Richness

Wetland area explained the greatest proportion of variation in each species richness estimate in semipermanent and seasonal wetlands (Tables 2-6). Wetland area alone accounted for 70.0-100% of explained variation in semipermanent wetlands and 55.1-100% of explained variation in seasonal wetlands. The percentage of vegetated wetland area was the next most common variable that explained >5% of variation in models (Tables 3-6). Waterfowl and nongame user bird species richness estimates were negatively associated with increasing coverage of emergent vegetation in semipermanent and seasonal wetlands (Tables 3-6). Dabbling duck species richness also was negatively associated with vegetated wetland area in seasonal wetlands (Tables 5 and 6). Nongame breeding bird species richness in semipermanent wetlands was the only estimate that related positively to vegetated wetland area (Tables 3 and 4).

The third variable that explained >5% of variation in species richness estimates was the proportion of untilled upland habitats within cells surrounding surveyed wetlands. Total waterfowl richness and dabbling duck species richness estimates in semipermanent wetlands were positively associated with untilled upland habitats (Tables 3 and 4). Lastly, nongame breeding bird species richness in seasonal wetlands was negatively associated with wetlands whose emergent hydrophytes were predominately thick-stemmed (e.g., cattail, river bulrush) and with wetlands that were partially or wholly surrounded by woody hydrophytes (e.g., willows) (Tables 5 and 6).

Habitat Variables Associated with Individual Species

Wetland area was the most frequent variable associated with the occurrence of individual species and was the first variable to enter the stepwise procedure for a majority of species in semipermanent and seasonal wetlands (Tables 7-10). Twenty of 21 species (95%) in semipermanent wetlands and 11 of 14 species (79%) in seasonal wetlands were positively associated with increasing wetland area. No species was negatively associated with wetland area. Vegetated wetland area was the second most frequent variable related

Table 2. Means ($\bar{X}$), standard errors (SE), and ranges of semipermanent and seasonal wetlands that were surveyed in eastern South Dakota, 1995-1996. A total of 412 semipermanent and 418 seasonal wetlands were surveyed. Calculations in this table were prior to data transformations. Summary statistics for seasonal wetlands are shown in parentheses. See Table 1 for descriptions of variables.

Variable[a]	$\bar{X}$	SE	Range
AREA	9.3(1.4)	1.3(0.1)	0.2-289.0(0.2-18.0)
TEMPA	81.4(85.4)	5.6(6.1)	0.9-1060.9(0.9-1060.9)
SEASA	66.1(67.2)	2.3(2.5)	2.8-325.2(2.8-325.2)
SEMIA	78.4(78.2)	6.0(8.3)	0-1371.6(0-1502.6)
PERMA	146.1(47.6)	41.8(6.4)	0-7683.7(0-797.4)
COVER	54.5(67.8)	1.6(1.4)	0.5-98.0(0.5-98.0)
SHORGR	53.6(61.6)	2.1(2.1)	0.5-98.0(0.5-98.0)
GRASS	0.5(0.5)	0.01(0.01)	0.11-0.99(0.11-0.99)
TREES	9.6(6.7)	1.1(1.0)	0-98.0(0-98.0)
VEGNUM	2.1(1.9)	0.05(0.04)	0-4(0-4)

STEM was a dummy-coded categorical variable indicating whether emergent hydrophytes within wetlands were predominately thick- or thin-stemmed.

Table 3. Habitat models that were generated using stepwise multiple regression analyses for eight species richness estimates of birds in semipermanent wetlands in eastern South Dakota, 1995-1996. Habitat variables included in models have $P \leq 0.05$ (see Table 4 for exact P values of individual variables). Variables were retained only when their inclusion explained an additional 5% of variation. Percentages in parentheses indicate the additional variation explained by each habitat variable. Total model R^2 is coefficient of determination for entire regression equation. The proportion of explained variance attributed to AREA is total model R^2 divided by AREA partial R^2, indicating the importance of habitat area. Variable definitions are in Table 1.

Richness Estimate	Habitat Model	Total Model R^2	% Explained Variance attributed to AREA
Total bird species	AREA	0.48	100.0
Total waterfowl	AREA - COVER + GRASS (0.35) (0.05) (0.05)	0.45	77.8
Total duck species	AREA	0.41	100.0
Dabbling ducks	AREA + GRASS (0.25) (0.05)	0.30	83.3
Diving ducks	AREA	0.28	100.0
Nongame breeder [a] bird species	AREA + COVER (0.28) (0.12)	0.40	70.0
Nongame user species [b]	AREA - COVER (0.26) (0.08)	0.34	76.5

'Nongame breeding species were defined as non-waterfowl wetland-obligate species that commonly nested in semipermanent and seasonal wetlands and spent most of the day using wetlands (Craig and Beal 1992).

[b]Nongame user species were defined as non-waterfowl species that foraged extensively in wetlands but which nested elsewhere.

Table 4. Estimated constants and coefficients (SE) for multiple regression analyses describing habitat models for species richness estimates of prairie wetland birds in semipermanent wetlands (see Table 3 for complete models). Predictor variables (Table 3) that did not enter habitat models for any richness estimates were excluded from this table. Coefficients are P<0.05 (asterisks indicate * $P < 0.01$, ** $P < 0.001$).

	Habitat Variable			
Richness Estimate	Constant	AREA	COVER	GRASS
Total bird species	1.64 (0.04)	0.36** (0.02)		
Total waterfowl	0.36 (0.16)	0.33** (0.03)	-0.01** (0.01)	0.88** (0.20)
Total duck species	1.46 (0.04)	0.34** (0.02)		
Dabbling ducks	0.08 (0.14)	0.27** (0.03)		0.82** (0.19)
Diving ducks	-0.06 (0.04)	0.24** (0.02)		
Nongame Breeders	0.72 (0.06)	0.31** (0.02)	0.01** (0.01)	
Nongame Users	0.88 (0.06)	0.26** (0.02)	-0.01** (0.01)	

Table 5. Habitat models that were generated using stepwise multiple regression analyses for seven species richness estimates of birds in seasonal wetlands in eastern South Dakota, 1995-1996. Habitat variables included in models have $P < 0.05$ (see Table 6 for exact P values of individual variables). Variables were retained only when their inclusion explained an additional 5% of variation. Percentages in parentheses indicate the additional variation explained by each habitat variable. Total model R^2 is coefficient of determination for entire regression equation. The proportion of explained variance attributed to AREA is total model R^2 divided by AREA partial R^2, indicating the importance of habitat area. Variable definitions are in Table 1.

Richness Estimate	Habitat Model	Total Model R^2	% Explained Variance attributed to AREA
Total bird species	AREA	0.27	100.0
Total waterfowl	AREA - COVER (0.20) (0.09)	0.29	69.0
Total duck species	AREA	0.25	100.0
Dabbling ducks	AREA - COVER (0.19) (0.07)	0.26	73.1
Nongame breeder [a] bird species	AREA - STEM - TREES (0.16) (0.07) (0.06)	0.29	55.1
Nongame user species [b]	AREA - COVER (0.10) (0.06)	0.16	62.5

[a] llongame breeding species were defined as non-waterfowl wetland-obligate species that commonly nested in semipermanent and seasonal wetlands and spent most of the day using wetlands (Craig and Beal 1992).

[b] Nongame user species were defined as non-waterfowl species that foraged extensively in wetlands but which nested elsewhere.

Table 6. Estimated constants and coefficients (SE) for multiple regression analyses describing habitat models for species richness estimates of prairie wetland birds in seasonal wetlands (see Table 5 for complete models). Predictor variables (Table 5) that did not enter habitat models for any richness estimates were excluded from this table. Coefficients are *$P<0.05$* (asterisks indicate *$P<0.01$, **$P < 0.001$).

	Habitat Variable				
	Constant	AREA	COVER	STEM	TREES
Richness Estimate[s]					
Total bird species	1.29 (0.04)	0.53**(0.05)			
Total waterfowl	0.99 (0.09)	0.47**(0.05)	-0.01**(0.01)		
Total duck species	1.13 (0.04)	0.49**(0.05)			
Dabbling ducks	1.97 (0.09)	0.45**(0.05)	-0.01**(0.01)		
Nongame breeder species	1.06 (0.05)	0.35**(0.04)		-0.33**(0.04)	-0.01**(0.01)
Nongame user species	0.72 (0.07)	0.32**(0.05)	-0.01**(0.01)		

aA species richness estimate was not calculated for diving ducks due to their minimal use of seasonal wetlands.

Table 7. Habitat models that were generated using stepwise logistic regression for 21 species of wetland birds in semipermanent wetlands in eastern South Dakota, 1995-1996. Habitat variables entered regression analyses at $P<0.15$ and were retained in the model when $P \leq 0.01$ (see Table 8 for slopes and exact P values of individual variables). Variables are listed in the order that they entered into the equation. Variable definitions are in Table 1.

Species	Habitat Model	[a] Number of Occurrences	McFadden's Rho-squared
Dabbling Ducks			
Mallard	- COVER + AREA	198	0.20
Blue-winged Teal	- COVER + AREA	246	0.18
Gadwall	AREA + GRASS	146	0.16
Northern Pintail	AREA + SEASA	76	0.15
Northern Shoveler	AREA - TREES	92	0.13
Diving Ducks			
Redhead	AREA + SEMIA + GRASS	82	0.20
Lesser Scaup	- COVER + AREA	50	0.20
Ruddy Duck	AREA	68	0.18
Geese			
Canada Goose	- COVER + LANDUSE + AREA + SEMIA - SEASA	36	0.27

[a] Sample sizes (number of semipermanent wetlands surveyed) were 324 for dabbling ducks and 412 for breeding nongame birds and divng ducks.

Table 7 (cont). Habitat models that were generated using stepwise logistic regression for 21 species of wetland birds in semipermanent wetlands in eastern South Dakota, 1995-1996. Habitat variables entered regression analyses at P<0.15 and were retained in the model when $P \leq 0.01$ (see Table 8 for slopes and exact P values of individual variables). Variables are listed in the order that they entered into the equation. Variable definitions are in Table 1.

Species	Habitat Model	[a] Number of Occurrences	McFadden's Rho-squared
Breeding Nongame Birds			
Eared Grebe	AREA - STEM	18	0.41
Black Tern	AREA + SEMIA + GRASS	106	0.24
American Bittern	COVER + AREA	34	0.21
Wilson's Phalarope	AREA - STEM + VEGNUM + **GRASS**	58	0.21
Marsh Wren	COVER + AREA + STEM	119	0.20
Pied-billed Grebe	AREA	120	0.19
Common Yellowthroat	COVER + AREA + SEMIA + STEM - GRASS	150	0.18
American Coot	AREA + STEM	206	0.17
Yellow-headed Blackbird	COVER + AREA + STEM	250	0.17
Sora	COVER - SHORGRAZ + AREA - SEMIA + VEGNUM	179	0.15
Virginia Rail	COVER + AREA + STEM	89	0.13
Red-winged Blackbird	- TREES + STEM	358	0.06

Table 8. Estimated constants and coefficients (SE) for stepwise logistic regression analyses describing habitat models for individual wetland birds in semipermanent wetlands (see Table 7 for complete models). Predictor variables (Table 7) that did not enter habitat models for any richness estimates were excluded from this table. Coefficients are P<0.01 (asterisks indicate*P < 0.001).

	Wetland Bird Species					
Habitat Variables	Mallard	Blue-winged Teal	Gadwall	Northern Pintail	Northern Shoveler	Redhead
Constant	-1.47 (0.41)	0.57 (0.48)	-4.45 (0.77)	-5.38 (1.00)	-2.01 (0.26)	-6.19 (0.93)
AREA	1.33*(0.21)	1.36*(0.26)	0.91*(0.14)	0.79*(0.14)	0.83*(0.14)	0.96*(0.13)
COVER	-0.01 (0.01)	-0.02 (0.01)				
GRASS			4.05*(0.97)			3.19 (1.09)
SEMIA						0.24 (0.09)
TREES					0.02 (0.01)	
SEASA				0.69 (0.23)		

Table 8 (cont). Estimated constants and coefficients (SE) for stepwise logistic regression analyses describing habitat models for individual wetland birds in semipermanent wetlands (see Table 7 for complete models). Predictor variables (Table 7) that did not enter habitat models for any richness estimates were excluded from this table. Coefficients are $P<0.01$ (asterisks indicate*$P < 0.001$).

	Wetland Bird Species					
Habitat Variables	Lesser Scaup	Ruddy Duck	Eared Grebe	Black Tern	American Bittern	Wilson's Phalarope
Constant	-2.27 (0.39)	-3.42 (0.31)	-4.88 (0.74)	-8.27 (0.98)	-5.63 (0.69)	-5.01 (1.00)
AREA	0.76*(0.14)	1.00*(0.14)	1.39*(0.25)	0.93*(0.13)	1.04*(0.16)	0.65*(0.14)
COVER	-0.03*(0.01)				0.02 (0.01)	
STEM			-2.11 *(0.63)			-2.14*(0.40)
GRASS				6.25*(1.10)		3.42 (1.27)
SEMIA				0.32*(0.09)		
VEGNUM						0.52 (0.18)

Table 8 (cont). Estimated constants and coefficients (SE) for stepwise logistic regression analyses describing habitat models for individual wetland birds in semipermanent wetlands (see Table 7 for complete models). Predictor variables (Table 7) that did not enter habitat models for any richness estimates were excluded from this table. Coefficients are $P<0.01$ (asterisks indicate $*P < 0.001$).

	Wetland Bird Species				
Habitat Variables	Marsh Wren	Pied-billed Grebe	Common Yellowthroat	American Coot	Yellow-headed Blackbird
Constant	-5.70 (0.72)	-2.74 (0.26)	-2.93 (0.79)	-2.30 (0.35)	-2.79 (0.42)
AREA	0.76*(0.14)	1.14*(0.14)	0.73*(0.13)	1.18*(0.15)	1.05*(0.16)
COVER	0.03*(0.01)		0.02*(0.01)		0.02*(0.01)
STEM	1.97*(0.53)		1.63*(0.41)	0.79 (0.30)	1.15*(0.31)
GRASS			-2.84*(0.87)		
SEMIA			0.21 (0.07)		

Table 8 (cont). Estimated constants and coefficients (SE) for stepwise logistic regression analyses describing habitat models for individual wetland birds in semipermanent wetlands (see Table 7 for complete models). Predictor variables (Table 7) that did not enter habitat models for any richness estimates were excluded from this table. Coefficients are P<0.01.

	Wetland Bird Species			
Habitat Variables	Sora	Virginia Rail	Red-winged Blackbird	Canada Goose
Constant	-2.00 (0.45)	-4.87 (0.66)	1.23 (0.27)	-0.34 (1.09)
AREA	0.41*(0.12)	0.57*(0.13)		0.71*(0.17)
COVER	0.02*(0.01)	0.03*(0.01)		-0.03*(0.01)
STEM		1.38 (0.51)	1.45* (0.33)	
SEASA				-1.17*(0.30)
SEMIA	-0.20 (0.07)			0.48*(0.13)
SHORGRAZ	-0.01 (0.01)			
LANDUSE				1.24 (0.44)
TREES			-0.02*(0.01)	
VEGNUM	0.42*(0.11)			

Table 9. Habitat models that were generated using stepwise logistic regression for 14 species of wetland birds in seasonal wetlands in eastern South Dakota, 1995-1996. Habitat variables entered regression analyses at $P<0.15$ and were retained in the model when $P \leq 0.01$ (see Table 10) for slopes and exact P values of individual variables). Variables are listed in the order that they entered into the equation. Variable definitions are in Table 1.

Species	Habitat Model	[a]Number of Occurrences	McFadden's Rho-squared
Dabbling Ducks			
Mallard	- COVER + AREA	132	0.11
Blue-winged Teal	AREA - COVER + SEMIA + SEASA	206	0.23
Gadwall	AREA + GRASS	95	0.07
Northern Pintail	AREA - STEM	57	0.14
Northern Shoveler	AREA - COVER	56	0.16
Breeding Nongame Birds			
Sora	COVER + AREA	142	0.09
Virginia Rail	STEM + COVER	38	0.09
Red-winged Blackbird	STEM + COVER - TREES	365	0.13

[a]Diving ducks (redhead, lesser scaup, and ruddy duck), Canada geese, eared grebes, black terns, and American bitterns were excluded from analyses due to their minimal use of seasonal wetlands.

Table 9 (cont). Habitat models that were generated using stepwise logistic regression for 14 species of wetland birds in seasonal wetlands in eastern South Dakota, 1995-1996. Habitat variables entered regression analyses at P<0.15 and were retained in the model when $P \leq 0.01$ (see Table 10 for slopes and exact *P* values of individual variables). Variables are listed in the order that they entered into the equation. Variable definitions are in Table 1.

Species	Habitat Model	'Number of Occurrences	McFadden's Rho-squared
Breeding Nongame Birds			
Wilson's Phalarope	AREA - STEM	51	0.13
Marsh Wren	STEM + COVER - SHORGRAZ + AREA + LANDUSE	50	0.19
Pied-billed Grebe	AREA	28	0.11
Common Yellowthroat	STEM + COVER - SHORGRAZ	87	0.14
American Coot	AREA + SEASA	81	0.07
Yellow-headed Blackbird	AREA + STEM + LANDUSE	102	0.18

[a]Diving ducks (redhead, lesser scaup, and ruddy duck), Canada geese, eared grebes, black terns, and American bitterns were excluded from analyses due to their minimal use of seasonal wetlands.

Table 10. Estimated constants and coefficients (SE) for stepwise logistic regression analyses describing habitat models for individual wetland birds in seasonal wetlands (see Table 9 for complete models). Predictor variables (Table 9) that did not enter habitat models for any richness estimates were excluded from this table. Coefficients are P<0.01 (asterisks indicate*P < 0.001).

	Wetland Bird Species					
Habitat Variables	Mallard	Blue-winged Teal	Gadwall	Northern Pintail	Northern Shoveler	Wilson's Phalarope
Constant	-0.07 (0.36)	-1.01 (0.84)	-4.26 (0.82)	-2.32 (0.28)	-2.89 (0.28)	-2.63 (0.28)
AREA	1.22*(0.24)	1.79*(0.36)	0.92*(0.23)	1.39*(0.25)	1.57*(0.25)	1.29*(0.24)
COVER	-0.02* (0.01)	-0.04 (0.01)				
SEMIA		0.22 (0.07)				
SEASA		0.58 (0.18)				
GRASS			3.68*(1.01)			
STEM				-0.99 (0.34)		-1.20*(0.37)

Table 10 (cont). Estimated constants and coefficients (SE) for stepwise logistic regression analyses describing habitat models for individual wetland birds in seasonal wetlands (see Table 9 for complete models). Predictor variables (Table 9) that did not enter habitat models for any richness estimates were excluded from this table. Coefficients are P<0.01 (asterisks indicate*P < 0.001).

	Wetland Bird Species			
Habitat Variables	Marsh Wren	Pied-billed Grebe	Common Yellowthroat	American Coot
Constant	-5.01 (0.75)	-3.86 (0.37)	-3.12 (0.49)	-4.14 (0.76)
AREA	1.10*(0.26)	1.37*(0.28)		0.82*(0.21)
COVER	0.02 (0.01)		-0.02*(0.01)	
STEM	1.36*(0.37)		1.60*(0.28)	
SEASA				0.52 (0.18)
SHORGRAZ	-0.01 (0.01)		-0.01 (0.01)	
LANDUSE	0.90 (0.36)			

Table 10 (cont). Estimated constants and coefficients (SE) for stepwise logistic regression analyses describing habitat models for individual wetland birds in seasonal wetlands (see Table 9 for complete models). Predictor variables (Table 9) that did not enter habitat models for any richness estimates were excluded from this table. Coefficients are $P<0.01$ (asterisks indicate*$P < 0.001$).

	Wetland Bird Species			
Habitat Variables	Yellow-headed Blackbird	Sora	Virginia Rail	Red-winged Blackbird
Constant	-3.16 (0.32)	-2.77 (0.38)	-4.86 (0.76)	0.95 (0.35)
AREA	1.15 *(0.22)	1.00*(0.21)		
COVER		0.02*(0.01)	0.03 (0.01)	0.01 (0.01)
STEM	1.47 (0.27)		-1.21*(0.38)	
LANDUSE	0.74 (0.26)			
TREES				-0.03 *(0.01)

to the occurrence of individual species in semipermanent (10 of 21 bird species) and seasonal (8 of 14 bird species) wetlands (Tables 7-10). The presence of each waterfowl species, for which vegetated wetland area was a significant predictor of occurrence, was negatively associated with vegetated wetland area (Tables 7-10). Conversely, vegetated wetland area was positively associated with the presence of each breeding nongame species for which it was a significant predictor of occurrence (Tables 7-10).

STEM was a dummy-coded categorical variable which indicated whether a particular bird species presence was related to the type of emergent hydrophytes in the wetland. A positive sign preceding STEM indicated that the bird species was positively associated with wetlands dominated by thick-stemmed plants. STEM was the third most frequent variable related to the occurrence of individual species in semipermanent (8 of 21 bird species) and seasonal (7 of 14 bird species) wetlands (Tables 7-10). Except for northern pintails, whose occurrence was negatively related to wetlands dominated by thick-stemmed emergents, breeding nongame birds were the only species related to the stem structure of vegetation. Occurrence of marsh wrens, common yellowthroats, American coots, yellow-headed and red-winged blackbirds, and Virginia rails in semipermanent and seasonal wetlands and American Coot in semipermanent wetlands was positively related to STEM (Tables 7-10). Occurrence of Wilson's phalarope in semipermanent and seasonal wetlands and eared grebes in semipermanent wetlands was negatively related to STEM (Tables 7-10).

Occurrence of six species in semipermanent wetlands and two species in seasonal wetlands was associated with total semipermanent or seasonal wetland area within cells surrounding surveyed wetlands. Four species (redhead, Canada goose, black tern, common yellowthroat) in semipermanent wetlands related positively and one species (sora) related negatively to total semipermanent wetland area within cells (Tables 7 and 8). Northern pintails in semipermanent wetlands related positively and Canada geese related negatively to total seasonal wetland area within cells. In seasonal wetlands, blue-winged teal related positively to total seasonal and semipermanent wetland areas within cells and American coot related positively only to total seasonal wetland area within cells (Tables 9 and 10).

Occurrence of two waterfowl species (gadwall, redhead) and two breeding nongame birds (black tern, Wilson's phalarope) in semipermanent wetlands was positively related to the proportion of untilled uplands in cells surrounding surveyed wetlands (Tables 7 and 8). One species, the gadwall, was positively associated with untilled upland habitat in semipermanent and seasonal wetlands. In semipermanent wetlands, common yellowthroat was the only species that the probability of occurrence was negatively associated with untilled upland habitat (Table 7). The three remaining variables (SHORGRAZ, LANDUSE, TREES) were associated with the occurrence of <3 species in either semipermanent or seasonal wetlands (Tables 7-10).

<u>Accuracy of Wetland Bird Surveys</u>

The accuracy assessment indicated that 93.3% of the wetland bird species that were recorded after two visits had already been detected during the first survey. No additional waterfowl or breeding nongame wetland bird species were detected when observers remained at smaller wetlands for a time equal to that spent at larger wetlands.

Discussion

Relationships between Species Richness/Occurrence and Wetland Area

The importance of wetland area, the predictor that accounted for the highest proportions of variation in species richness estimates, was apparent in analyses for individual species as occurrence of 95% of wetland-obligate bird species in semipermanent and 79% of species in seasonal wetlands was positively associated with increasing wetland area. Only red-winged blackbirds and soras, two of the most abundant and cosmopolitan wetland species, used wetlands without regard to habitat area. An assessment of minimum wetland area requirements for individual species and an evaluation of the effects of wetland isolation in landscapes which differ in total wetland densities and areas are the focus of Chapter 2.

The Influence of Emergent Wetland Vegetation Abundance and Structure

Vegetation Preferences of Waterfowl.--Vegetative preferences of individual species were reflected in the total waterfowl species richness estimate that was negatively related to vegetated wetland area in semipermanent and seasonal wetlands. Increased probabilities of occurrence of mallard, blue-winged teal, and northern shoveler were evident in wetlands with intermediate cover-to-open water ratios (38-63% median vegetated area) compared to wetlands whose surface area was predominated by emergent vegetation (98% median vegetated area). High correlations ($r > 0.5$) between cover type classifications (Stewart and Kantrud 1971), a measure of the distribution of emergent vegetation within wetlands, and the proportion of vegetated wetland area indicated that distribution of emergent vegetation and total vegetated area were linked; intermediate cover-to-open water ratios corresponded to cover type classifications with the highest vegetation interspersion (i.e., cover types 2 and 3).

Similar relationships between the occurrence of dabbling ducks and vegetation-water interspersion found in this study have been widely reported (Weller and Spatcher 1965, Kaminski and Prince 1981, 1984). Kaminski and Prince (1981, 1984) found that higher dabbling duck densities and species diversity were related to the effects that vegetation-water interspersion had on forage availability and isolation space for breeding pairs. In the present study, a 3-fold increase in mallard occurrence in semipermanent (66% versus 21% occupancy) and seasonal (56% versus 18%) wetlands with intermediate cover-to-open water ratios (38-63% median vegetated area) compared to wetlands that lacked open water areas (98% median vegetated area) attested to the importance of habitat interspersion to breeding dabbling ducks.

Lesser scaup and Canada geese, two species whose occurrence in semipermanent wetlands were used in waterfowl species richness calculations, also related negatively to vegetated wetland area. Although the increased occurrence of lesser scaup in wetlands with intermediate cover-to-open water ratios may be related to invertebrate abundance and diversity (Bartonek and Hickey 1969, Sugden 1973, Siegfried 1976), Canada goose occurrence in more sparsely vegetated semipermanent wetlands may have reflected timing of season in which surveys were conducted. Less densely vegetated wetlands that were used by geese during brood-rearing may have provided open water habitat for predator avoidance (Lee et al. 1984).

Vegetation Preferences of Breeding Nongame Bird Species.--Vegetative preferences of individual species were reflected in a breeding nongame bird species richness estimate that was positively related to vegetated semipermanent wetland area. While the occurrence of species in semipermanent wetlands was not negatively associated with vegetated wetland area, species whose probability of occurrence was positively related to greater coverage of emergent vegetation (sora, marsh wren, American bittern, Virginia rail, yellow-headed blackbird, common yellowthroat) were those typically found in dense, closed stands of emergent vegetation (Faanes 1982, Gibbs et al. 1991, Melvin and Gibbs 1994, Twedt and Crawford 1995).

Occurrence of eight of 12 species that were related to structural attributes of emergent wetland vegetation reflected the divergent life history requirements of breeding nongame birds. Individual species associations with vegetation abundance and structure in seasonal wetlands were similar to those in semipermanent wetlands. Four of six species (marsh wren, yellow-headed and red-winged blackbirds, common yellowthroat) whose occurrence was positively associated with semipermanent wetlands that were dominated by thick-stemmed emergent plants (STEM) were species that depend on structure provided by robust emergent vegetation to support the weight of aerial, over-water nests. Positive relationships of American coots and Virginia rails to wetlands with thick-stemmed emergents probably reflects their need for nest-building materials or concealment cover (Alisauskas and Arnold 1994, Conway 1995). Eared grebes also commonly nested in wetlands dominated by thin-stemmed emergent plants while the occurrence of Wilson's phalaropes was negatively associated with thick-stemmed emergent vegetation. Wilson's phalaropes prefer foraging sites that include more open water habitats or those dominated by thin-stemmed emergent plants (Colwell and Jehl 1994).

Vegetation Preferences of User Nongame Bird Species.--A diverse assemblage of bird species that foraged extensively in semipermanent (n=19 species with >10 occurrences) and seasonal (n=8) wetlands, but nested elsewhere, were negatively associated with increasing coverage of emergent wetland vegetation (user bird species richness). Models identifying factors associated with species occurrence were not defensible because user species may have opportunistically exploited wetlands for food resources (e.g., schooling fish, macroinvertebrates), a factor that was not quantified in this study; however, the prevalence of ardeids (e.g., great blue heron, black-crowned night-heron), shorebirds (e.g., killdeer), and piscivorous species (e.g., double-crested cormorant and American white pelican *[Pelecanus erythrorhynchos])* indicated that mudflats and expanses of open water areas devoid of emergent vegetation were important habitat features for foraging birds.

<u>The Influence of Upland Habitat on the Occurrence of Wetland Birds</u>

Ball et al. (1995) found that duck productivity in Montana was highest in large, unfragmented grasslands with relatively low predator populations. Although productivity was not directly quantified in this study, higher dabbling duck species richness and an increased incidence of gadwalls were found in wetlands located within landscapes with higher proportions of untilled uplands. Greenwood et al. (1987) reported that dabbling duck nest success was correlated positively with the proportion of grassland in their study sites in southern Canada. Average proportion of untilled uplands (cells) in this study was 10.4% higher near semipermanent wetlands in which dabbling duck species richness was at a maximum compared to wetlands that were devoid of dabbling ducks.

Relationships between grassland abundance and the occurrence of upland nesting species (i.e., gadwall, Wilson's phalarope) are more easily understood than those of over-water nesting species such as redheads and black terns, which also were more likely to nest in areas composed predominately of untilled uplands. Despite a current lack of understanding concerning mechanisms linking upland vegetation to wetland functions (Van der valk 1989), many species (i.e., gadwall, Wilson's phalarope, redhead, black tern) associated with untilled upland area in this study were more likely to occur in wetlands with surrounding uplands that were <50% tilled. Clark et al. (1991) found that duck productivity may be unpredictable when predation is a major cause of nest failures despite the establishment of moderately large (50-200 ha) grasslands; however, continued placement and maintenance of grassland cover is an important waterfowl management objective until the influence of grassland area on duck production has been fully assessed.

CHAPTER 2

ESTIMATING HABITAT AREA REQUIREMENTS OF PRAIRIE WETLAND BIRDS

Introduction

Numerous other investigators (e.g., Evans and Black 1956, Drewien and Springer 1969, McEnroe 1976, Rumble and Flake 1983) have concluded that dabbling duck use of prairie wetlands was positively related to wetland area and Brown and Dinsmore (1986, 1988), working in 30 marshes in a wetland impoverished area of northwest Iowa, have previously reported that bird density and species richness was positively related to wetland area. Despite the importance of references indicating that bird use and species richness typically increase with increasing wetland area, previous researchers have lacked the necessary sample sizes required to quantify minimum habitat area requirements of prairie wetland birds.

Results from large-scale studies that were designed to quantify minimum habitat area requirements for birds in forests (e.g., Askins et al. 1987, Temple and Cary 1988, Robbins et al. 1989) and prairie remnants (e.g., Samson 1980, Herkert 1994) have been used in preserve design and development. Therefore, to further investigate the importance of wetland area on bird species occurrence in semipermanent and seasonal wetlands in this study, I examined relationships between wetland area and the probabilities of occurrence of individual species to obtain estimates of the minimum wetland area needed for species breeding in the prairie pothole region. In addition to calculating minimum area requirements, I also determined minimum wetland areas required to preserve multiple area-dependent wetland species and investigate the importance of the more than 228,000 (Johnson and Higgins 1997) small (<1-ha in area) semipermanent and seasonal wetlands to breeding wetland avifauna in eastern South Dakota.

Study Area and Methods

The study area for this chapter and the methods used to select semipermanent and seasonal wetlands that were surveyed in this study occur in the Study Area and Methods sections of Chapter 1. Chapter 1 Methods also describe characteristics used to define the four landscape types used in this study.

Using Logistic Analyses to Estimate Wetland Area Requirements

Logistic regression (Cox 1970, Wilkinson 1997) was used to estimate minimum wetland areas necessary to ensure adequate breeding habitat for 20 wetland bird species whose probability of occurrence was positively associated with semipermanent or seasonal wetland area (Chapter 1). As in Chapter 1, data from both years were pooled for all analyses after a preliminary comparison of breeding bird species richness did not reveal significant differences between years ($P > 0.10$). I restricted use of species occurrence data in this analysis to wetlands with intermediate cover-to-water ratios (median vegetated wetland area 38-63%) (Brown and Dinsmore 1986), which corresponded to the "hemi-marsh phase" (Weller and Spatcher 1965, Weller and Fredrickson 1974), the wetland phase with the greatest bird species richness and density (Gibbs et al. 1991). Specifically, wetlands with intermediate cover-to-water ratios were selected to ensure that 1) open water areas were available within wetlands for waterfowl species that were negatively associated with vegetated wetland area, to 2) provide nesting habitat for breeding nongame species that were positively associated with vegetated wetland area (Chapter 1), and 3) to enable grouping of multiple species within wetlands for later analyses.

For this analysis, the model

$$P(y_i = 1) = \frac{\exp(\beta_0 + \beta_1 x_{1i})}{1 + \exp(\beta_0 + \beta_1 x_{1i})}$$

was used where P (y_i = 1) is the probability of the particular species being present in wetland i and po and p, (the natural logarithm of wetland area), are model parameters to be estimated. Significance of the regression was tested using the Wald chi-square statistic (maximum likelihood estimate). McFadden's Rho-squared statistic was used to evaluate model fit. Semipermanent and seasonal wetlands were analyzed separately.

Predicted probabilities of occurrence generated by logistic analyses (95% confidence intervals) were plotted against wetland area for species whose probability of occurrence increased significantly with increasing area. The 50% probability of occurrence was used as a conservative estimate of the minimum area required by a species (Robbins et al. 1989, Herkert 1994). Estimated wetland area at the 50% probability of occurrence was used to subjectively rank area-dependency of each bird species as high (?15 ha), moderate (5-14.9 ha), and low (0.2-4.9 ha). Species whose occurrence was not related to wetland area were considered area-independent species.

Wetlands used in analyses also were sorted to determine area of the smallest wetland in which a particular species occurred. The proportion of occupied wetlands was calculated as the number of semipermanent or seasonal wetlands containing an individual species divided by the number of wetlands with intermediate cover-to-water ratios.

Bird Occurrence within Differing Landscape Types

For species for which both wetland area and total area of semipermanent (SEMIA) or seasonal (SEASA) wetlands within cells were associated with an individual species occurrence (Chapter 1), I tested the effects of the latter variables on the relationship between a species probability of occurrence and wetland area. Logistic analyses were conducted separately for each species in the four types of landscapes (Fig. 3) described in Chapter 1. Predicted probabilities of occurrence were plotted by landscape type for each species whose overall probability of occurrence was associated with total semipermanent or seasonal wetland area within cells. Semipermanent and seasonal wetland analyses were conducted separately using species occurrence information from every wetland surveyed.

Probability Theory and the Importance of Small Wetlands

Predicted probabilities of occurrence from original analyses with wetlands having intermediate cover-to-water ratios were used to evaluate whether several small wetlands could equal or approximate the importance of a single large wetland for conserving area-dependent wetland birds. A formula for computing the number of 0.5-ha, 1-ha, 3-ha, and 5-ha wetlands that would have to surveyed to have the same probability of detecting a particular species in a semipermanent wetland of an area in which the probability of occurrence was at a maximum was adapted from Robbins et al. (1989) where:

P_{max} = P (particular species is detected in > 1 wetland of x ha)

= 1 - P (particular species is not detected in any of n wetlands of x ha)

= 1 - (1 - P_x)°.

where:

$$n = \frac{\log(1 - P,)}{\log(1 - P_x)}$$

Actual number of occurrences of a particular species in wetlands of x ha also were recorded.

Probability of Detecting Multiple Area-dependent Species.

Logistic regression also was used to examine the relationship between wetland area and the probability of detecting at least x number of the 18 area-dependent species in semipermanent wetlands or the seven area-dependent species in seasonal wetlands (listed as to area-dependency in Table 11). For semipermanent wetlands, the number of area-dependent species within wetlands were tallied and each wetland was assigned either a zero or one value for each of 18 variables, indicating whether or not at least 1, 2, 3....18 of the 18 area-dependent species were detected. Each of 18 variables was used as the dependent variable in separate logistic regressions, with the natural logarithm of wetland area as the independent variable in each regression. The likelihood ratio chi-square statistic was used to evaluate significance of regressions. Species occurrences from every semipermanent wetland surveyed were included in analyses to 1) evaluate minimum wetland area needed to provide breeding habitat for multiple wetland species regardless of vegetated wetland area, and 2) to meet minimum sample size restrictions. Logistic regression analyses for the seven area-dependent species in seasonal wetlands were conducted in the same manner as described above for species in semipermanent wetlands.

Results

Classifying Wetland Bird Area-dependency

The probabilities of occurrence of 18 bird species in semipermanent wetlands and seven species in seasonal wetlands increased with increasing wetland area (Table 11). The likelihood ratio chi-square statistic testing the association of probability of occurrence and wetland area was significant ($P<0.01$) for each regression. In semipermanent wetlands, five species (lesser scaup, American bittern, eared grebe, Wilson's phalarope, Virginia rail) (see Appendix 1 for scientific names not listed in text) were classified as highly area-dependent because their probabilities of occurrence at 50% of the maximum (suggested minimum area) were >15 ha (Tables 11 and 12; Fig. 5). Eight species (northern pintail, ruddy duck, marsh wren, black tern, northern shoveler, redhead, common yellowthroat, pied-billed grebe) whose 50% probabilities of occurrence were between 5-ha and 14.9-ha were classified as moderately area-dependent (Tables 11 and 12; Fig. 6) while area-dependency for five species (gadwall, American coot, mallard, yellow-headed blackbird, blue-winged teal) was low (50% probability of occurrence was 0.2-4.9 ha) (Fig. 7). Soras and red-winged blackbirds, two of the most commonly

Table 11. Habitat area-dependency of 20 wetland birds using semipermanent and seasonal prairie wetlands. Logistic regression was used to estimate area-dependency for species whose probability of occurrence increased with area. Minimum area requirements were delineated as those at which the probability of a species occurrence was 50% of the maximum. Species whose occurrence was not related to area were area-independent. Area of the smallest wetland in which a species occurred is in parentheses. The proportion of occupied wetlands (% occurrence) is the number of wetlands occupied divided by the number of wetlands in the hemi-marsh condition (50% vegetated, 50% open water).

	Area-dependency		Area at 50% Probability		% Occurrence	
Species	Semipermanent	Seasonal	Semipermanent	Seasonal	Semipermanent	Seasonal
Lesser Scaup	High		164.8 (1.4)		10	
American Bittern	High		117.6 (1.5)		8	
Eared Grebe	High		95.1 (10.0)		4	
Wilson's Phalarope	High	Independent	87.0 (0.3)	(0.3)	17	13
Virginia Rail	High	Independent	55.5 (0.3)	(0.2)	20	8
Northern Pintail	Moderate	Low	25.9 (0.6)	3.3 (0.3)	5	25
Ruddy Duck	Moderate		20.8 (0.9)		20	
Marsh Wren	Moderate	Moderate	14.5 (0.5)	7.8 (0.2)[a]	29	8
Black Tern	Moderate		12.4 (0.3)		33	
Northern Shoveler	Moderate	Low	11.1 (0.4)	2.7 (0.2)	12	27
Redhead	Moderate		9.2 (0.6)		27	
Common Yellowthroat	Moderate	Independent	8.8 (0.6)	(0.2)	34	17
Pied-billed Grebe	Moderate	Moderate	5.7 (0.7)	6.4 (0.2)	36	9
Gadwall	Low	Independent	2.6 (0.4)	(0.2)	33	39
American Coot	Low	Moderate	1.7 (0.3)	5.0 (0.2)	60	25
Mallard	Low	Low	1.0 (0.3)	0.5 (0.2)	38	57
Yellow-headed Blackbird	Low	Moderate	0.8 (0.2)	5.2 (0.2)	67	23
Blue-winged Teal	Low	Independent	0.3 (0.3)	(0.2)	64	80
Sora	Independent	Independent	(0.2)	(0.2)	45	30
Red-winged Blackbird	Independent	Independent	(0.2)	(0.2)	88	85

[a]Maximum probability of occurrence for marsh wrens in seasonal wetlands was 0.40.

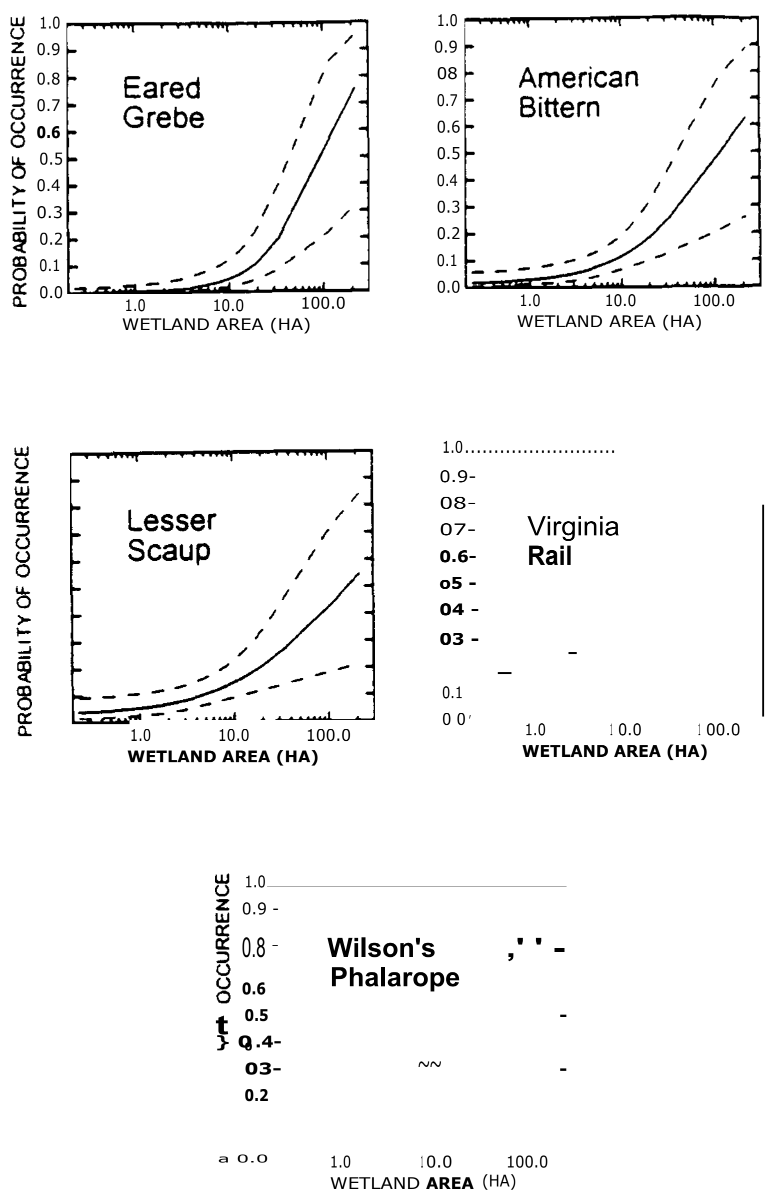

Fig. 5. Probabilities of detecting five highly area-dependent wetland species in semipermanent wetlands of various areas. Dotted lines are 95% confidence intervals for the predicted probabilities.

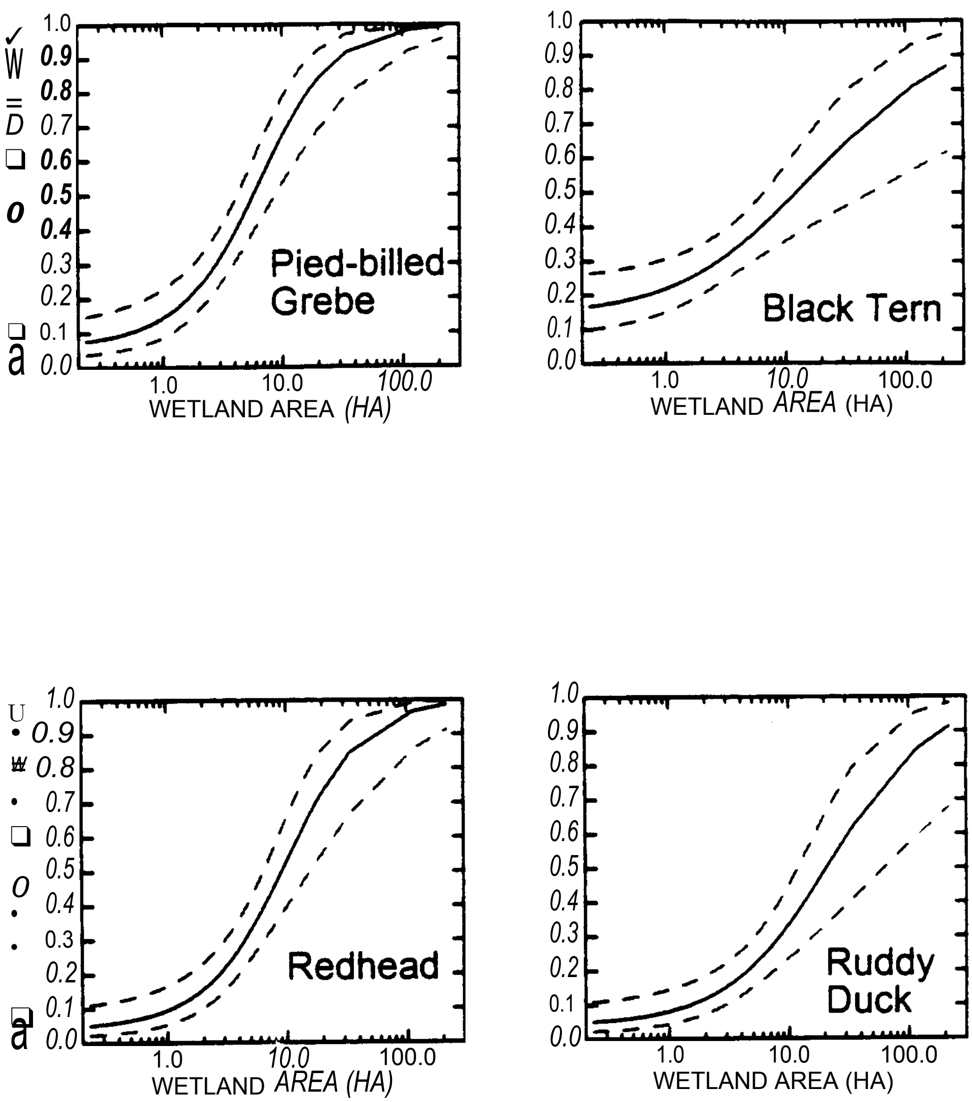

Fig. 6. Probabilities of detecting eight moderately area-dependent wetland species in semipermanent wetlands of various areas. Dotted lines are 95% confidence intervals for the predicted probabilities.

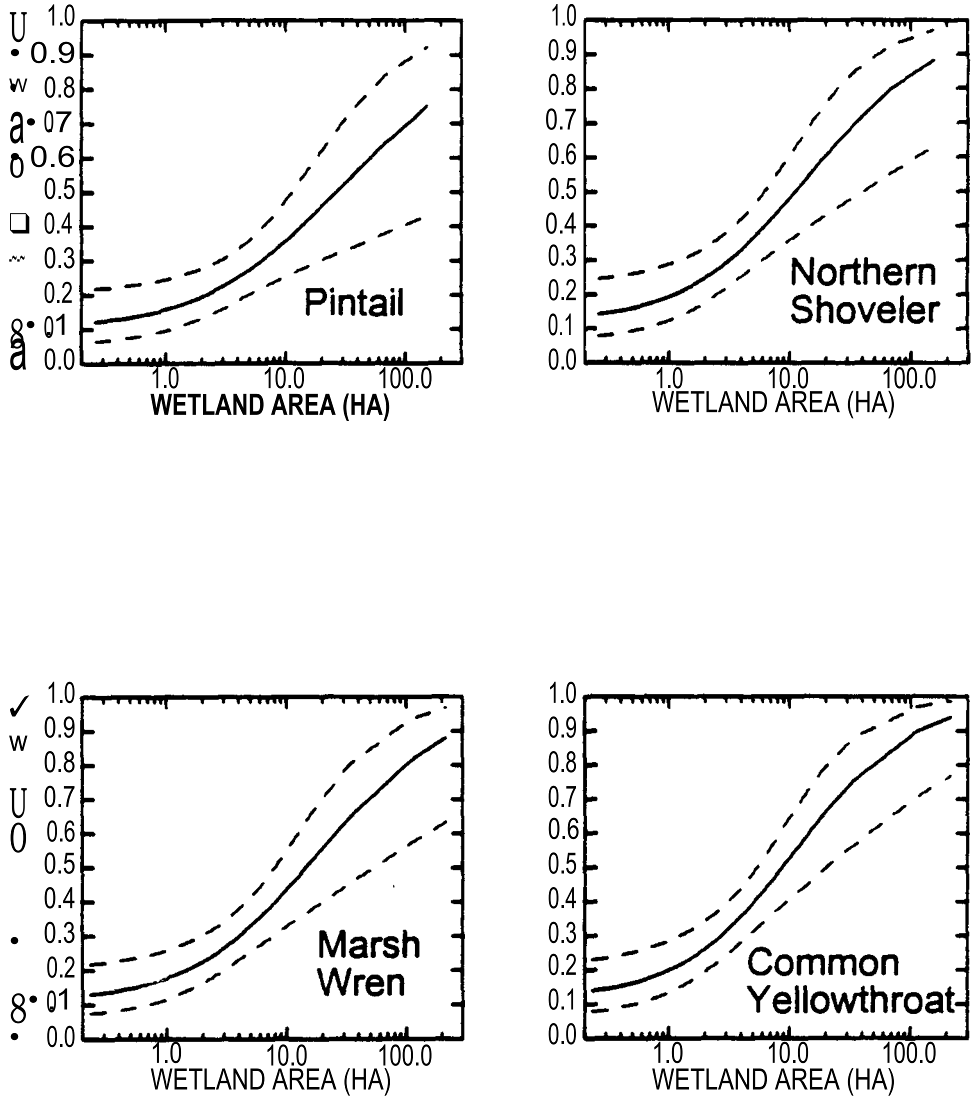

Fig. 6 (cont). Probabilities of detecting eight moderately area-dependent wetland species in semipermanent wetlands of various areas. Dotted lines are 95% confidence intervals for the predicted probabilities.

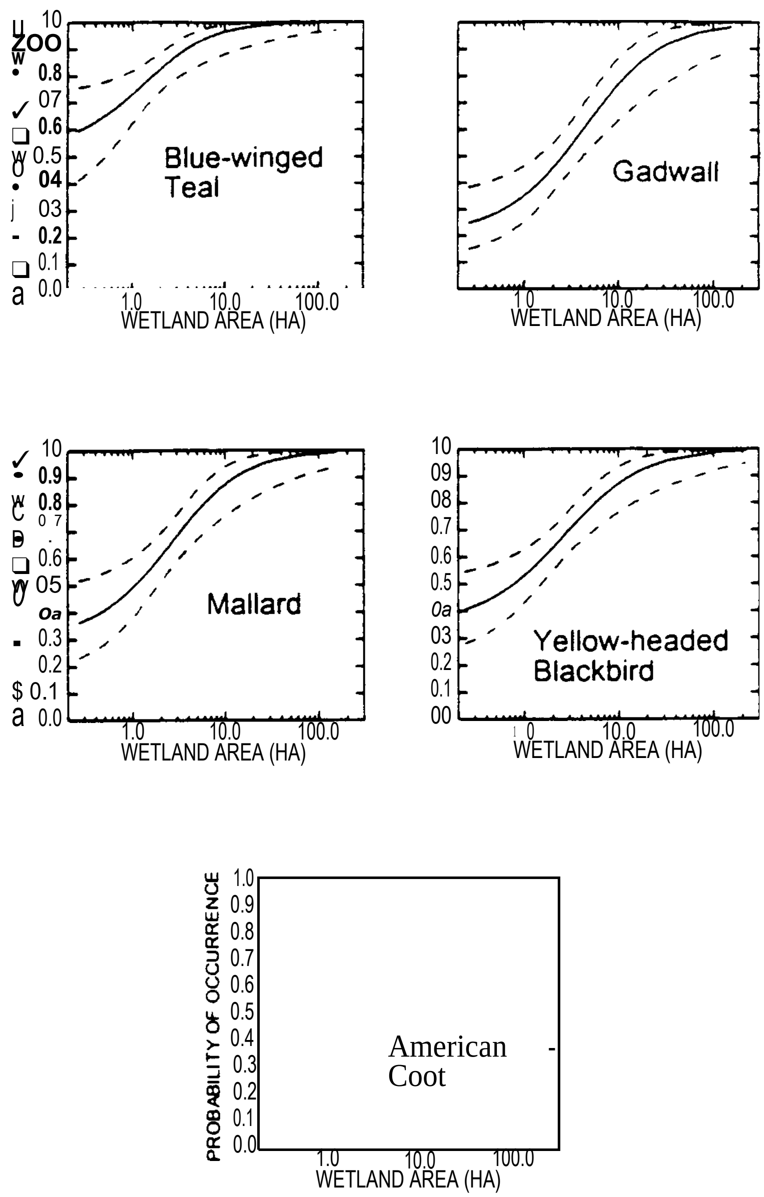

Fig. 7. Probabilities of detecting five wetland species whose area-dependency was low in semipermanent wetlands. Dotted lines are 95% confidence intervals for the predicted probabilities.

Table 12. Estimated coefficients and McFaddens's Rho-squared values for logistic regression analyses. Independent variable is wetland area. Dependent variable is binary, based on the occurrence of each particular bird species within semipermanent wetlands. Likelihood ratio chi-square statistic testing the association of probability of occurrence and wetland area was significant (P<0.01) for each species listed. Red-winged blackbird and sora were excluded from the table because their occurrence was not associated (P>0.05) with wetland area.

Species	Intercept	Slope	McFadden's Rho-squared
Lesser Scaup	-3.324	0.652	0.09
American Bittern	-4.091	0.857	0.15
Eared Grebe	-6.281	1.375	0.37
Wilson's Phalarope	-2.468	0.551	0.06
Virginia Rail	-2.358	0.585	0.07
Northern Pintail	-2.123	0.639	0.07
Ruddy Duck	-3.137	1.019	0.17
Marsh Wren	-2.062	0.752	0.10
Black Tern	-1.748	0.673	0.08
Northern Shoveler	-1.977	0.789	0.10
Redhead	-3.212	1.384	0.24
Common Yellowthroat	-2.009	0.882	0.12
Pied-billed Grebe	-2.809	1.472	0.24
Gadwall	-1.356	1.057	0.13
American Coot	-1.444	1.439	0.19
Mallard	-0.834	1.151	0.13
Yellow-headed blackbird	-0.601	1.046	0.11
Blue-winged Teal	-0.069	1.362	0.13

detected birds during surveys (Table 11), were classified as area-independent species because their probability of occurrence was unrelated to wetland area (P>0.05).

No species was classified as highly area-dependent in seasonal wetlands because the largest seasonal wetlands surveyed were <15 ha in area. Overall mean area for seasonal wetlands surveyed in this study was 1.4 ha (SE = 0.10) compared to mean semipermanent wetland area of 9.3 ha (SE = 1.30) (Table 2). Three highly area-dependent species (lesser scaup, American bittern, eared grebe) and three moderately area-dependent species (ruddy duck, redhead, black tern) in semipermanent wetlands occurred on <5% of seasonal wetlands. Black terns were excluded from seasonal wetland analyses because, although they foraged extensively on seasonal wetlands, nest searches indicated that tems nested in <1% of seasonal wetlands.

Four species (marsh wren, pied-billed grebe, American coot, yellow-headed blackbird) in seasonal wetlands were classified as moderately area-dependent because their probabilities of occurrence at 50% of the maximum were between 5-ha and 14.9-ha (Tables 11 and 13; Fig. 8). The area-dependency of three species (northern pintail, northern shoveler, mallard) was low (50% probability of occurrence was 0.2-4.9 ha) (Fig. 9). Seven species (Wilson's phalarope, Virginia rail, gadwall, blue-winged teal, common yellowthroat, sora, red-winged blackbird), five of which were area-dependent species in semipermanent wetlands, were classified as area-independent species in seasonal wetlands because their probability of occurrence was unrelated to wetland area (P>0.05).

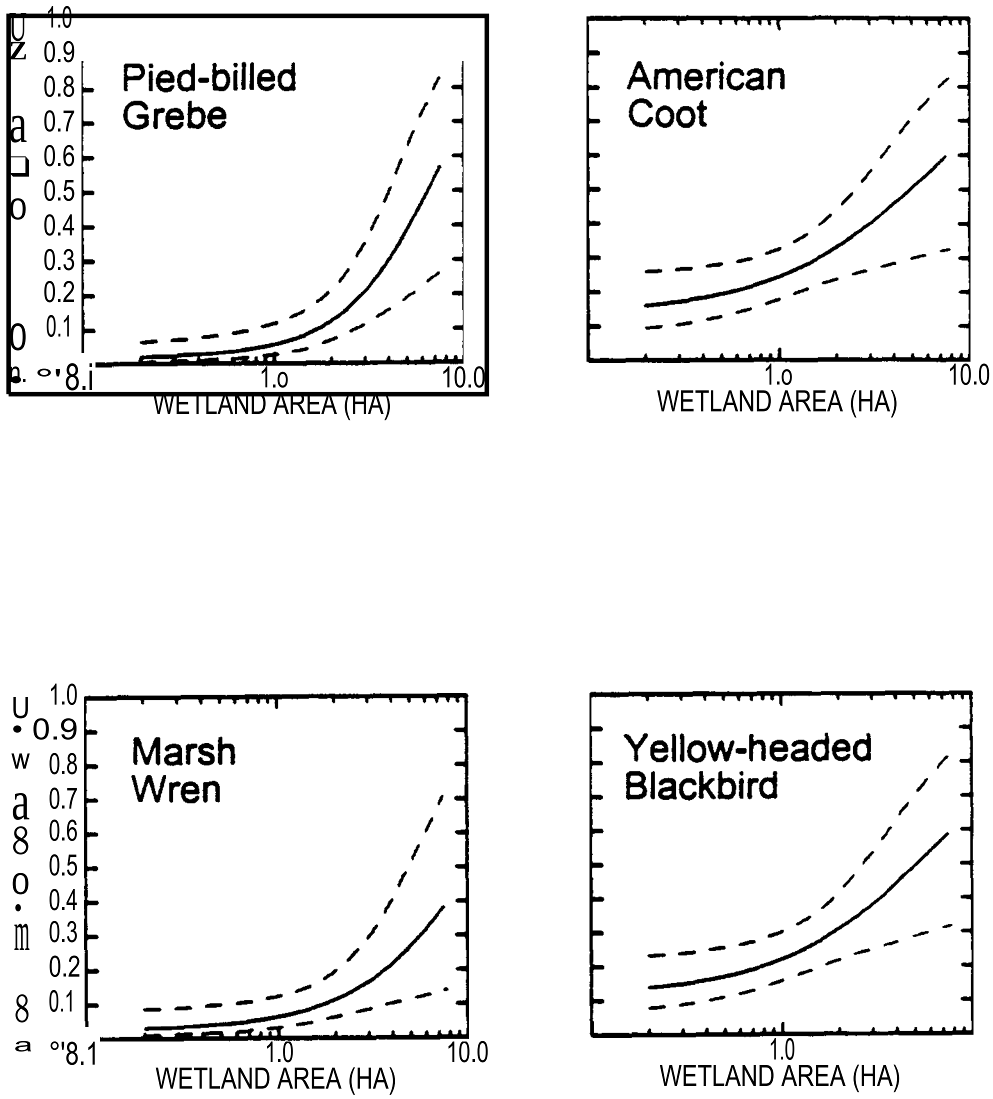

Fig. 8. Probabilities of detecting four moderately area-dependent wetland species in seasonal wetlands of various areas. Dotted lines are 95% confidence intervals for the predicted probabilities.

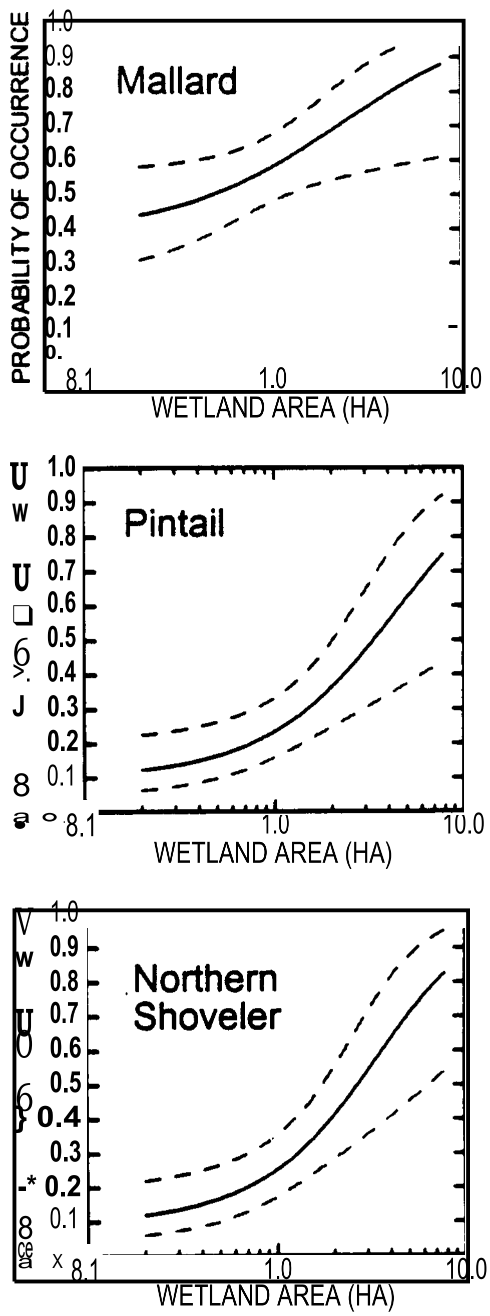

Fig. 9. Probabilities of detecting three wetland species whose area-dependency was low in seasonal wetlands. Dotted lines are 95% confidence intervals for the predicted probabilities.

Table 13. Estimated coefficients and McFaddens's Rho-squared values for logistic regression analyses. Independent variable is wetland area. Dependent variable is binary, based on the occurrence of each particular bird species within seasonal wetlands. Likelihood ratio chi-square statistic testing the association of probability of occurrence and wetland area was significant ($P<0.01$) for each species listed. Species that occurred too infrequently or whose occurrence in seasonal wetlands was not associated ($P>0.05$) with wetland area were excluded from this table (see Table 9 for specific species).

Species	Intercept	Slope	McFadden's Rho-squared
Northern Pintail	-2.248	1.535	0.10
Marsh Wren	-3.755	1.533	0.10
Northern Shoveler	-2.328	1.786	0.13
Pied-billed Grebe	-4.315	2.149	0.19
American Coot	-1.853	1.048	0.05
Mallard	-0.452	1.118	0.04
Yellow-headed blackbird	-2.034	1.118	0.05

Bird Occurrence within Landscapes

Logistic analyses were conducted separately in the four landscape types (Chapter 1; Fig. 3) for the seven species in which both wetland area and total area of semipermanent (SEMIA) or seasonal (SEASA) wetlands within cells were associated with an individual species occurrence (Chapter 1; Tables 7 and 9). Predicted probabilities that were plotted by landscape type indicated that minimum area requirements of black terns in semipermanent wetlands and American coots in seasonal wetlands may fluctuate within differing wetland landscapes (Fig. 10). Slopes from predicted probabilities between landscape types for species other than black terns and American coots commonly overlapped. Minimum wetland area requirements (50% probability of occurrence) for black terns were 6.5 ha in landscaped (Wald x^2=29.61, ldf, P<0.001) (Fig. 10), 15.4 ha in landscape c (Wald x^2=17.10, ldf, P<0.001), and 32.6 ha in landscape *b* (Wald x^2=5.44, ldf, P=0.020). The 50% cut-off point was never reached for black terns in landscape a (Wald x^2=1.54, ldf, P=0.215) (Fig. 10). Area requirements for American coots were 3.2 ha in landscaped (Wald x^2=11.10, ldf, P=0.001) (Fig. 10), 6.8 ha in landscape c (Wald x^2=3.15, ldf, P =0.076), and 13.5 ha in landscape *b* (Wald x^2=5.20, ldf, P=0.023). The 50% cut-off point was never reached for American coots in landscape a (Wald x^2=1.90, ldf, P=0.168) (Fig. 10).

Bird Use of Small Wetlands

The number of small semipermanent and seasonal wetlands (<0.5 ha) that would have to be surveyed before detection probabilities were equal to maximum detection rates in large wetlands (i.e., approaching $_{Pmax)}$ for most breeding nongame bird species are

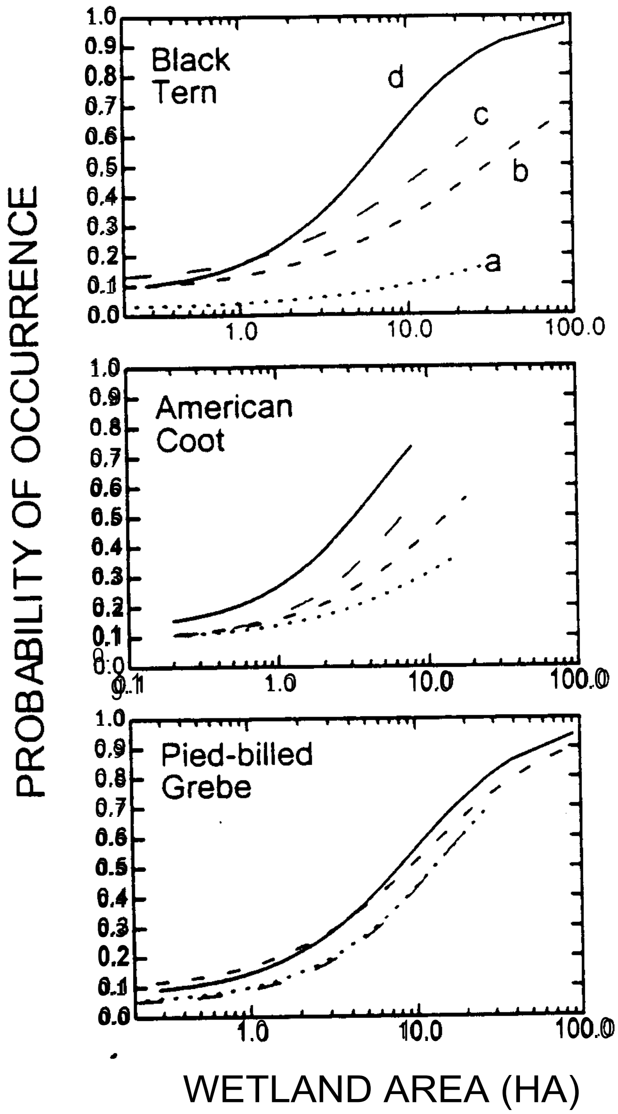

Fig. 10. Probabilities of detecting black terns and American coots in four landscape types (Fig. 3) (see text for explanation).

presented in Tables 14 and 15. The absence or low number of occurrences (<3) of many species in 0.5- and 1.0-ha semipermanent wetlands and 0.2- to 0.5-ha seasonal wetlands (Tables 14 and 15) indicated that the collective areas of several small wetlands do not equal that of a larger wetland for most area-dependent species. For instance, eared grebes and American bitterns did not occur or were present on <5% of semipermanent wetlands < 5 ha (Table 14). Pied-billed grebes and marsh wrens did not occur or were present on <5% of seasonal wetlands 0.2- to 0.5-ha in area (Table 15). Multiple 3- and 5-ha semipermanent wetlands or 1- and 2-ha seasonal wetlands may approximate the value of a single large wetland with regard to occurrence probabilities for several area-dependent species (Tables 14 and 15).

Positive relationships existed between wetland area and the probability of detecting multiple area-dependent species within semipermanent and seasonal wetlands (Figs. 11 and 12). Estimated coefficients for the probabilities of finding >16 area dependent species in semipermanent wetlands are in Table 16 ($P<0.002$ for each regression). Estimated coefficients for the probabilities of finding >6 area dependent species in seasonal wetlands are in Table 17 ($P<0.006$ for each regression). Minimum areas of semipermanent and seasonal wetlands necessary to provide suitable breeding habitat to area-dependent species increased with an increasing number of species (Figs. 11 and 12). The probability of finding at least one area-dependent species was high in semipermanent (0.79 in wetlands >0.2 ha area) and seasonal wetlands (0.54 in wetlands >0.5 ha area) (Figs. 11 and 12). The probability of detecting >16 species in semipermanent wetlands or >6 species in seasonal wetlands was low (<0.10) in 98.0 and

Table 14. The number of 0.5-ha, 1-ha, 3-ha, and 5-ha semipermanent wetlands that would have to be surveyed for the probability of detecting each of 18 area-dependent bird species to be the same as in one wetland of the area at which probability of occurrence is at a maximum (P_m). Brackets indicate that the species did not occur in any wetlands of that area and parentheses indicate that the species occurred in <5% of wetlands of a given area.

		Number of Wetlands			
Species	Pmax	0.5-ha	1-ha	3-ha	5-ha
Lesser Scaup	0.56	[16.9]	[12.3]	(3.6)	1.3
American Bittern	0.65	(108.8)	(27.2)	(5.3)	(1.3)
Eared Grebe	0.78	[1878.6]	[205.5]	[13.8]	[1.5]
Wilson's Phalarope	0.63	(9.4)	7.3	2.7	1.2
Virginia Rail	0.70	(10.3)	(7.7)	2.8	1.2
Northern Pintail	0.79	[10.4]	7.6	2.6	1.1
Ruddy Duck	0.92	[36.4]	(22.3)	3.9	1.2
Marsh Wren	0.89	(13.0)	9.4	2.8	1.2
Black Tern	0.87	(9.4)	7.1	2.5	1.2
Northern Shoveler	0.91	(12.0)	9.1	2.7	1.2
Redhead	0.99	[60.6]	(31.3)	3.6	1.2
Common Yellowthroat	0.94	[14.9]	10.0	2.7	1.1
Pied-billed Grebe	0.99	[45.5]	(22.5)	1.5	1.2
Gadwall	0.99	(12.7)	8.3	2.3	1.2
American Coot	0.99	(11.7)	6.7	1.6	1.0
Mallard	0.99	8.0	5.3	1.7	1.0
Yellow-headed Blackbird	0.99	6.3	4.9	1.7	1.0
Blue-winged Teal	0.99	4.3	2.8	1.2	1.0

Table 15. The number of 0.2-ha, 0.5-ha, 1-ha, and 2-ha seasonal wetlands that would have to be surveyed for the probability of detecting each of seven area-dependent bird species to be the same as in one wetland of the area at which probability of occurrence is at a maximum (P_{m}.). Brackets indicate that the species did not occur in any wetlands of that area and parentheses indicate that the species occurred in <5% of wetlands of a given area.

		Number of Wetlands			
Species	Pmax	0.2-ha	0.5-ha	1-ha	2-ha
Marsh Wren	0.40	(15.9)	(10.4)	4.9	1.3
Pied-billed Grebe	0.59	[44.0]	(23.1)	(8.2)	1.3
Yellow-headed Blackbird	0.60	(6.1)	4.5	2.7	1.2
American Coot	0.61	(53.8)	4.0	2.5	1.2
Northern Pintail	0.75	(10.4)	6.8	3.5	1.2
Northern Shoveler	0.83	(13.9)	8.4	3.9	1.2
Mallard	0.88	3.7	2.8	2.0	1.1

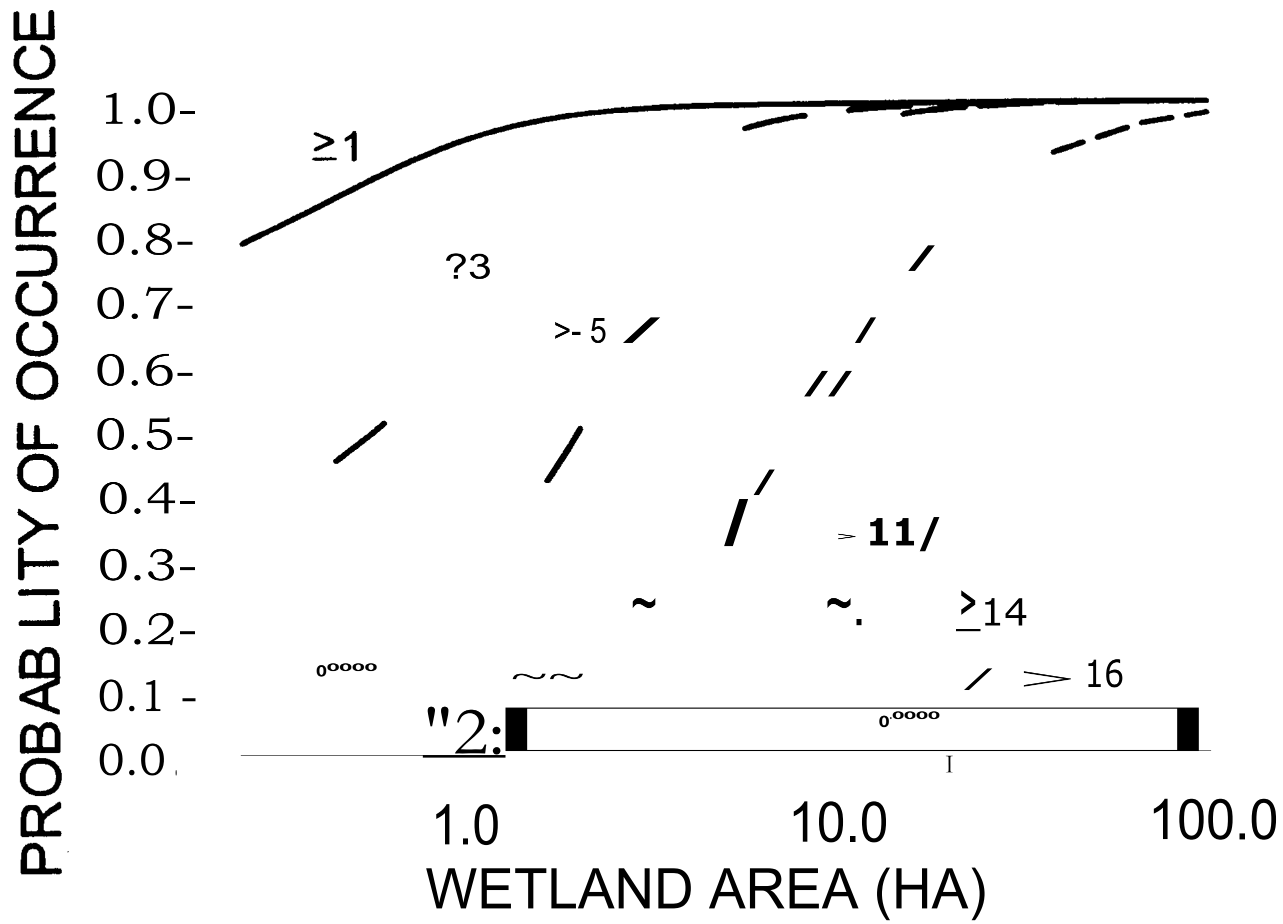

Fig. 11. Probabilities of detecting at least 1, 3, 5, 8, 11, 14, and 16 area-dependent bird species in semipermanent wetlands of various areas.

Table 16. Estimated coefficients and McFaddens's Rho-squared values for logistic regression analyses. Independent variable is wetland area. Dependent variable is binary, based on the number of area-dependent bird species that occurred within semipermanent wetlands. Likelihood ratio chi-square statistic testing the association of probability of occurrence and wetland area were significant ($P<0.002$) for each regression. The 18 area-dependent species used in analyses are in Table 11. Maximum number of area-dependent species occurring in any single semipermanent wetland was 16.

Number of Area-dependent Species	Number of Wetlands Containing the Specified Number of Species	Intercept	Slope	McFadden's Rho-squared
>1	312	0.573	3.324	0.21
>2	288	-0.612	2.956	0.25
>3	257	-1.014	2.235	0.24
>4	217	-2.366	2.735	0.34
>5	187	-2.685	2.410	0.34
>6	154	-2.733	1.897	0.30
>7	120	-3.155	1.716	0.30
>8	94	-3.647	1.668	0.31
>9	74	-4.015	1.591	0.32
>10	50	-4.810	1.607	0.35
>11	38	-5.191	1.553	0.36
>12	29	-5.140	1.346	0.32
>13	16	-6.197	1.399	0.36
>14	12	-6.788	1.451	0.38
>15	6	-8.845	1.738	0.48
>16	3	-7.776	1.236	0.27

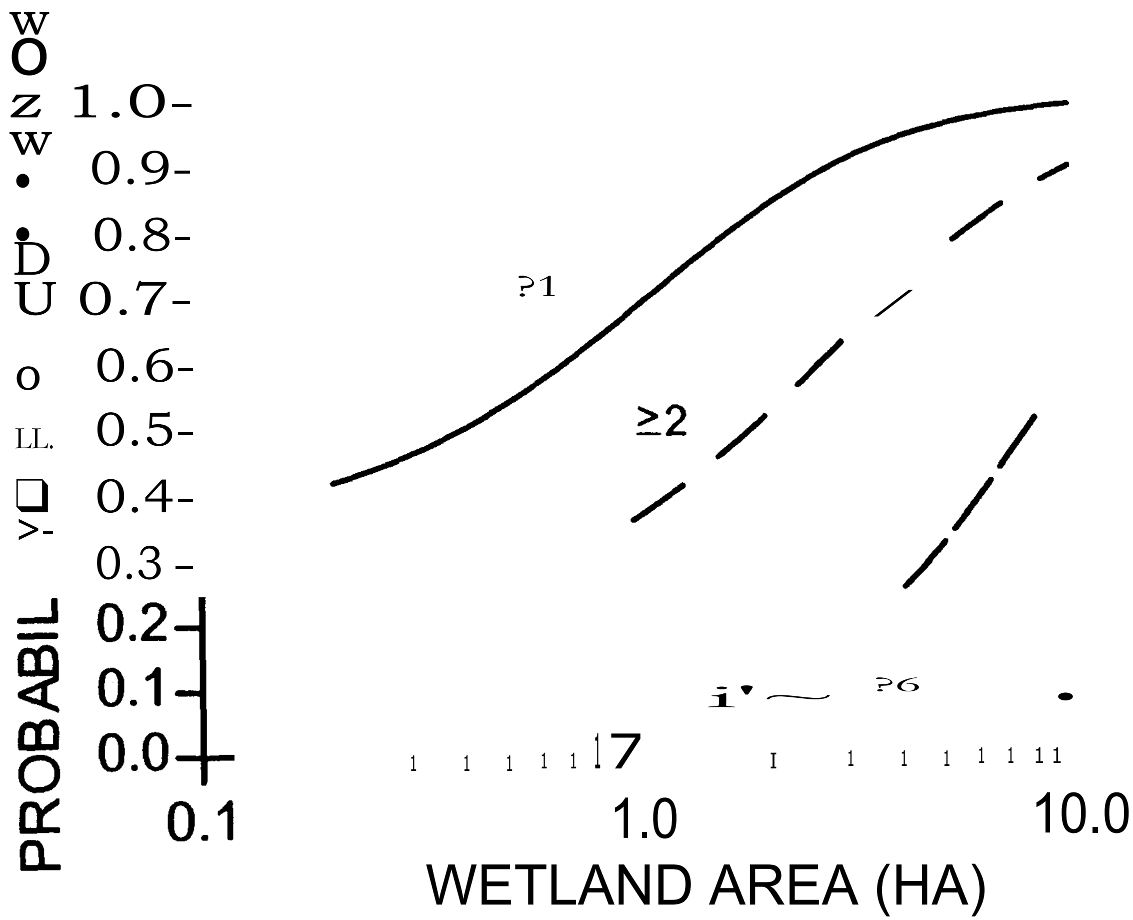

Fig. 12. Probabilities of detecting at least 1, 2, 4, and 6 area-dependent bird species in seasonal wetlands of various areas.

Table 17. Estimated coefficients and McFaddens's Rho-squared values for logistic regression analyses. Independent variable is wetland area. Dependent variable is binary, based on the number of area-dependent bird species that occurred within seasonal wetlands. Likelihood ratio chi-square statistic testing the association of probability of occurrence and wetland area were significant (P<0.006) for each regression. The seven area-dependent species used in analyses are in Table 11. Maximum number of area-dependent species occurred in any single seasonal wetland only once.

Number of Area-dependent Species	Number of Wetlands Containing the Specified Number of Species	Intercept	Slope	McFadden's Rho-squared
>1	208	-0.724	2.161	0.12
>2	121	-1.674	1.608	0.12
>3	63	-2.960	1.842	0.19
>_4	29	-4.208	1.933	0.23
	18	-4.677	1.803	0.21
>6	3	-6.995	1.957	0.22

98.4% of wetlands surveyed. No semipermanent wetland contained >16 of 18 area-dependent species. The maximum number (n=7) of area-dependent species was found in only one seasonal wetland.

Discussion

Area Requirements of Prairie Wetland Birds

Species-area relationships were not simply an artifact of sampling (Connor and McCoy 1979), because accuracy assessments (Chapter 1) indicated that length of time observers spent within wetlands did not influence the number of species detected and that single surveys effectively characterized wetland bird communities. High bird detection rates using single surveys in a large number of wetlands over an extensive geographic region enabled sample size requirements of logistic analyses to be met. Estimates of minimum area requirements were derived from wetlands with intermediate cover-to-open water ratios to ensure that area-dependency was not artificially inflated due to inclusion of wetlands that did not meet vegetation needs of particular species. For instance, preliminary analyses using all surveyed wetlands without regard to vegetated wetland area indicated that blue-winged teal, gadwall, Wilson's phalaropes, and soras were area-dependent in either seasonal or semipermanent wetlands; however, occurrence of these species was unrelated to wetland area when only wetlands with intermediate cover-to-open water ratios were used in analyses.

Wetland area, which was the most important predictor of species occurrence in regression analyses (Chapter 1), strongly influenced the composition of breeding wetland bird communities. Smaller semipermanent wetlands were predominately occupied by area-independent species and by species whose area-dependency was low (0.2-4.9 ha) while larger wetlands generally had a higher diversity, composed of species whose area requirements ranged from 0.2-164.8 ha. Direct comparisons of area estimates between this study and others was not possible because occurrence of species in previous studies (Brown and Dinsmore 1986, Gibbs et al. 1991) was plotted against area classes using incidence functions (Diamond 1975). Nevertheless, area estimates using logistic analyses in this study are in general agreement with categorical wetland area classes for most species (Brown and Dinsmore 1986, Gibbs et al. 1991). Discrepancies between wetland area estimates from this study and those from Brown and Dinsmore (1986) were apparent for dabbling ducks (blue-winged teal, mallard, gadwall) whose minimum wetland area requirements (50% probability of occurrence) in semipermanent and seasonal wetlands in South Dakota were smaller than those in Iowa. Estimates of minimum area requirements derived from presence/absence data should be interpreted cautiously until long-term demographic information (e.g., reproductive success), which is largely lacking for species other than waterfowl, is obtained to further evaluate the dynamics that influence long-term population viability (Van Home 1983, Pulliam 1988, Vickery et al. 1992).

Influence of Landscape Types on Wetland Area Requirements

Seven species whose occurrence was positively associated with total areas of semipermanent and seasonal wetlands within 25.9 km' cells indicated that wetland species diversity was greater when wetlands were located within wetland complexes. The occurrence of five of the seven species (blue-winged teal in seasonal wetlands and northern pintail, redhead, Canada goose, and common yellowthroat in semipermanent wetlands) that related positively to the total areas of semipermanent or seasonal wetlands within cells apparently were not influenced by the four types of wetland complexes defined in this study (Landscape Types *a, b, c, d;* Fig. 3); however, area requirements of two species (black terns in semipermanent wetlands and American coots in seasonal wetlands) were related to wetland landscape types.

Farmer and Parent (1997) recently related increased foraging efficiencies of shorebirds to compositional attributes of wetland landscapes. They concluded that pectoral sandpipers *(Calidris melanotos)* reduced energetic costs associated with searching for prey while foraging in landscapes containing multiple closely spaced wetlands (Farmer and Parent 1997). Occurrence of black terns in this study, a species that regularly travels up to 4-km away from its nesting wetland to forage (Dunn and Agro 1995), also was highly dependent on the prevalence and diversity of semipermanent wetlands near the nesting wetland. Logistic analyses in this study indicated that black terns are an area-dependent species whose wetland area requirements may fluctuate in response to compositional attributes of the wetland landscape. Wetlands in Landscape a, a low wetland density landscape composed of primarily small wetlands, where few nesting wetlands occurred and potential food sources were spread over large distances, were not widely used by black terns. In contrast, black tern wetland area requirements in landscape *d,* a high wetland density landscape containing a mixture of large and small wetlands, were small (6.5 ha) compared to those in more homogeneous landscapes composed of predominately large (Landscape c; 32.6 ha) or small wetlands (Landscape b; 15.4 ha). Black tern use of larger wetlands in Landscapes *a, b,* and c was not an artifact of wetland availability because pied-billed grebes, whose minimum area requirements were essentially identical to those of black terns in Landscape d (Fig. 10), occurred on semipermanent wetlands of similar area regardless of landscape type (Fig. 10).

The Importance of Small Wetlands

Highest diversity of breeding nongame birds and waterfowl in this study was found in three of the largest semipermanent (70.2-217.5 ha) and seasonal wetlands (1.6-6.9) surveyed. Although the larger wetlands may contain higher numbers of species, most of the 76,260 semipermanent and 334,699 seasonal wetlands that compose -60% of the nearly 900,000 ha of wetland area in eastern South Dakota (Johnson and Higgins 1997) are small in area. Median area of semipermanent and seasonal wetlands is 0.92 and 0.20 ha, respectively, with 93% of seasonal wetlands <2 ha in area (Johnson and Higgins 1997). Lower minimum area requirements and higher average occupancy rates of seasonal wetlands compared to semipermanent wetlands by mallard, gadwall, blue-winged teal, northern pintail, and northern shoveler indicated that small seasonal wetlands provided extensive breeding habitat for dabbling duck populations. Kantrud and Stewart (1977) reported that seasonal wetlands contained 60% of the population of dabbling ducks in the prairie pothole region of North Dakota. Unfortunately, small, seasonal wetlands in agricultural landscapes are among the most common types of wetlands at high risk of drainage (Johnson et al. 1996). The value of seasonal wetlands in this study should not decrease the importance of semipermanent wetlands, because dabbling ducks that prefer smaller seasonal wetlands early in the season move to larger semipermanent wetlands later in the season as seasonal wetlands dry (Keith 1961, Stoudt

1969, Kantrud and Stewart 1977). Wetland surveys for this study were conducted during years when seasonal wetlands remained wet throughout much of the summer; however, the relative value of seasonal wetlands may decrease in dry years when dabbling duck habitat is in semipermanent wetlands (Kantrud and Stewart 1977).

In addition to their importance to dabbling ducks, small seasonal wetlands also provided habitat comparable to that of large semipermanent wetlands for three species of breeding nongame birds. Wilson's phalaropes, Virginia rails, and common yellowthroats, whose area-dependency was moderate to high on semipermanent wetlands, occurred almost as frequently in seasonal wetlands without regard to wetland area (i.e., area-independent). Discrepancies in area-dependency of Wilson's phalaropes and Virginia rails in seasonal and semipermanent wetlands may be related to water depth which influences availability of foraging sites. Occurrence of Wilson's phalaropes and Virginia rails was independent of habitat area in small seasonal wetlands, which often lack more open, deep-marsh zones that are typical of semipermanent wetlands (Stewart and Kantrud 1971, Kantrud and Stewart 1984), but still provide preferred shallow-water foraging habitats (Rundle and Fredrickson 1981, Weber et al. 1982, Conway 1995, Colwell and Jehl 1994). In contrast, use of larger semipermanent wetlands (i.e., highly area-dependent in semipermanent wetlands) by Wilson's phalaropes and Virginia rails reflected their preference for feeding areas in shallow marsh zones surrounding deeper-water habitats within semipermanent wetlands, rather than a genuine need for larger wetlands.

<u>Preserving Multiple Area-dependent Species</u>

To this point, only relationships between wetland area and the probability of detecting individual species have been discussed. A positive relationship between wetland area and the probability of finding multiple area-dependent species indicated that bird species diversity increased with increasing wetland area. In semipermanent wetlands, probabilities of detecting at least five area-dependent species in wetlands 0.5-ha, 1-ha, 3-ha, and 5-ha in area were 0.15, 0.27, 0.65, and 0.84 , respectively (Fig. 11). Likewise, the probabilities of detecting at least 1, 3, 5, and 8 area-dependent species in a wetland 0.92 ha in area, the median area of semipermanent wetlands in eastern South Dakota (Johnson and Higgins 1997), were 0.94, 0.60, 0.24, and 0.07, respectively.

Over the range of semipermanent wetlands surveyed (0.3-217.5 ha), the probability of finding at least eight area-dependent species in an 8-ha semipermanent wetland exceeded 0.50 using area as the sole management criterion. In addition to their usefulness in predicting the number of species in a given wetland, probability curves also provide guidelines for evaluating potential benefits of wetland protection when multiple wetlands which differ in area are being considered for acquisition. Results from this study indicate that when the number of area-dependent species in semipermanent wetlands is >4, a factor of 1.5 (SE = 0.05) may be used to determine how much larger a wetland of x area must be to support another area-dependent species. For example, an 8-ha wetland containing eight area-dependent species would only need to be four hectares larger in area (8 ha multiplied by 1.5 = 12 ha) to contain one additional species whereas a 16-ha wetland would need to be eight hectares larger, twice that of the 8-ha wetland, for an additional species to be present. If wetland position within landscapes also is considered, wetlands of this area or smaller may provide breeding habitat for species whose minimum area requirements decrease when nest wetlands are near other wetlands (e.g., black tern).

Analyses designed to determine whether several small wetlands could approximate the value of a large wetland indicated that several small wetlands, no matter how well placed within landscapes, cannot provide suitable habitat for numerous wetland-obligate species that only nest in large wetlands. For example, American bitterns, eared grebes, and lesser scaup were surveyed on <5% of 5-ha semipermanent wetlands. Similarly, an absence or low occurrence of pied-billed grebes and marsh wrens in small seasonal wetlands indicated that conservation efforts to preserve habitat for these species should target seasonal wetlands >0.50-ha in area. Occurrence probabilities did indicate that multiple 3- to 5-ha semipermanent wetlands or multiple 1- to 2-ha seasonal wetlands may provide some breeding habitat for species whose area-dependency is moderate to low.

Managing Landscapes for Wetland Bird Diversity

High rates of wetland loss and degradation, which are negatively impacting wetland-obligate bird populations (e.g., Ball et al. 1994), have prompted a need for large-scale studies that direct wetlands conservation over broad geographic regions and compliment what has been learned at local scales (Flather and Sauer 1996). Despite the need for this type of research, managers continue to extrapolate recommendations from local studies to regional levels because few studies have taken a landscape-level approach to designing research. Recent advances in geographic information systems and remote sensing technologies, now enable wildlife researchers to use sampling strategies that allow valid and more reliable inferences to be made over larger landscapes. Results of the present study, which were derived from a representative sample of >800 wetlands across six major physiographic regions, may reliably be applied to the 36,000 semipermanent and seasonal wetlands (Johnson and Higgins 1997) in eastern South Dakota, and possibly to wetlands throughout the northern Great Plains. To my knowledge, this study also provides the only empirical information concerning minimum habitat area requirements for wetland birds, an attribute which estimates the likelihood of providing for even minimum populations of individual species, an important component in developing prescriptive management or preservation strategies for wetlands conservation.

The obvious management recommendation from this research is to preserve large semipermanent wetlands that have the highest probability of providing habitat for the least common, most area-dependent species. However, to preserve large wetlands without considering the importance of small wetlands would leave most landscapes in the northern Great Plains unprotected from drainage and degradation because only 7% of seasonal wetlands are >5 ha in area and only 29% of semipermanent wetlands are >10 ha in area (Johnson and Higgins 1997). Therefore, rather than simply concentrating preservation efforts on large semipermanent wetlands that occur within limited geographic areas, minimum area estimates from this study also can be used to prioritize wetland acquisitions in landscapes dominated by small, seasonal wetlands.

I recommend that high priority be given to the protection of large semipermanent wetlands that are embedded in large, contiguous tracts of upland grasslands since minimum area estimates indicate that these wetlands are the only wetlands large enough to support breeding populations of species requiring the greatest wetland area. In instances where protection of the largest semipermanent wetlands is not an option, but managers are presented with an opportunity to acquire a number of smaller semipermanent wetlands, my analysis of the importance of small wetlands has indicated that numerous small, semipermanent wetlands will provide some breeding habitat for target species whose area dependency is moderate to low. Alternatively, if management goals are not intended to preserve the most area-dependent species, but are designed simply to provide for any number of area-dependent species, managers can simply refer to Figure 11 to find out how many area-dependent species will likely occur within a semipermanent wetland of a given size.

The identification of five area-independent nongame species (Wilson's phalarope, Virginia rail, sora, common yellowthroat, red-winged blackbird) in this study indicated that every seasonal wetland, regardless of its size, represents valuable breeding habitat for some wetland avifauna. Results from this study also indicated that, in addition to providing habitat for multiple nongame species, small seasonal wetlands embedded within grassland-dominated landscapes also provide extensive dabbling duck habitat during wet hydrologic conditions (Rotella and Ratti 1992). Therefore, I also recommend that wetland managers give high priority to preserving the abundance of small seasonal wetlands that occur within grassland-dominated landscapes throughout the areas of eastern South Dakota, which are largely devoid of semipermanent wetlands (Higgins and Johnson 1997).

Results from this study also indicated that multiple species use seasonal wetlands within agricultural landscapes where upland grasslands were largely lacking. Although several authors (e.g., Clark and Nudds 1991) have questioned the importance of these wetlands to upland nesting waterfowl, Higgins et al. (1996) recently reported that waterfowl brood production in the Central Lowlands, one of the most intensively cultivated regions of eastern South Dakota, was higher than that in the Prairie Coteau or Missouri Coteau regions during wet years when seasonal wetlands retained water during the breeding season. Therefore, to devalue wetlands in intensively-farmed areas may be presumptive when bird production in such habitats is high during wet years.

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Appendix 1. Common and scientific names of species used to calculate species richness estimates (Chapter 1) for birds in semipermanent (A) and seasonal (B) wetlands in eastern South Dakota, 1995-1996. Species that occurred in > 10 wetlands were included in richness estimates.

		Richness Estimate						
Common Name	Latin Name	Total Bird Species	Total Waterfowl	Total Duck Species	Dabbling Ducks	Diving Ducks	Nongame Breeders	Nongame Users
Mallard	***Anas platyrhynchos***	AB	AB	AB	AB			
Gadwall	***Anas*** *strepera*	AB	AB	AB	AB			
Northern Pintail	***Anas acuta***	AB	AB	AB	AB			
Blue-winged Teal	***Anas discors***	AB	AB	AB	AB			
Northern Shoveler	*Anas clypeata*	AB	AB	AB	AB			
Redhead	*Aythya americana*	AB	AB	AB		A		
Canvasback	*Aythya valisineria*	A	A	A				
Lesser Scaup	*Aythya afnis*	A	A	A		A		
Ring-necked Duck	*Aythya collaris*	A	A	A		A		
Ruddy Duck	*Oxyura jamaicensis*	A	A	A		A		
Canada Goose	*Branta canadensis*	A	A					
Eared Grebe	*Podiceps nigricollis*	A					A	
Pied-billed Grebe	*Podilymbus podiceps*	AB					AB	
Black Teri	*Chlidonias niger*	A					A	
American Bittern	*Botaurus lentiginosus*	AB					AB	
Virginia Rail	*Rallus limicola*	AB					AB	
Sora	*Porzana carolina*	AB					AB	
American Coot	*Fulica americana*	AB					AB	
Wilson's Phalarope	*Phalaropus tricolor*	AB					AB	
Common Yellowthroat	*Geothlypis trichas*	AB					AB	
Marsh Wren	*Cistothorus palustris*	AB					AB	

Appendix 1 (cont). Common and scientific names of species used to calculate species richness estimates (Chapter 1) for birds in semipermanent (A) and seasonal (B) wetlands in eastern South Dakota, 1995-1996. Species that occurred in > 10 wetlands were included in richness estimates.

		Richness Estimate						
Common Name	Latin Name	Total Bird Species	Total Waterfowl	Total Duck Species	Dabbling Ducks	Diving Ducks	Nongame Breeders	Nongame Users
Red-winged Blackbird	*Agelaius phoeniceus*	AB					AB	
Yellow-headed Blackbird	***Xanthocephalus xanthocephalus***	AB					AB	
Swamp Sparrow	*Melospiza georgiana*	A					A	
Tree Swallow	*Tachycineta bicolor*	AB						
Bank Swallow	*Riparia riparia*	A						A
Barn Swallow	***Hirundo rustica***	AB						AB
Cliff Swallow	*Hirundo fulva*	AB						AB
Common Grackle	*Quiscalus quiscula*	AB						AB
Brown-headed Cowbird	*Molothrus ater*	AB						AB
Killdeer	*Charadrius vociferus*	AB						AB
Franklin's Gull	*Larus pipixcan*	A						A
Upland Sandpiper	*Bartramia longicauda*	A						A
Marbled Godwit	*Limosa fedoa*	A						A
Willet	*Catoptrophorus semipalmatus*	A						A
Double-crested Cormorant	*Phalacrocorax auritus*	A						A
Great Blue Heron	*Ardea herodius*	A						A
Black-crowned Night-heron	*Nycticorax nycticorax*	A						A
Sedge Wren	*Cistothorus platensis*	A						A
Song Sparrow	*Melospiza melodia*	AB						AB
Savannah Sparrow	*Passerculus sandwichensis*	A						A
Eastern Kingbird	*Tyrannus tyrannus*	AB						AB